GROWTH OF CHUM SALMON IN RELATION TO POPULATION ABUNDANCE AND CLIMATE IN THE EASTERN NORTH PACIFIC OCEAN AND THE RECRUITMENT OF POLLOCK IN THE EASTERN BERING SEA

By

Ellen Martinson Yasumiishi

RECOMMENDED:

Dr. John Helle

Dr. Nicola Hillgruber

Dr. Franz Mueter

Dr. Keith Criddle, Advisory Committee Chair

Dr. Shannon Atkinson
Chair, Graduate Program, Fisheries Division

APPROVED:

Dr. Michael Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger
Dean of the Graduate School

10/29/2013
Date

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A

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Ellen Martinson Yasumiishi, B.S., M.S.

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Abstract

Global climate change is expected to change the distribution and growth of marine species. Therefore, understanding how climate, ocean productivity, and population abundance affect the dynamics of marine species will help predict how growth and recruitment of marine species will respond to future changes in climatic and oceanic conditions. Statistically significant intertemporal correlations have been observed between a variety of environmental factors and recruitment, growth, mortality, and abundance of fish populations. However, because these correlative relationships are not reflective of the actual biophysical processes, the relationships can break down, particularly when used for forecasting. Failure of these simple correlative relationships motivates the search for biological indicators that integrate ocean productivity across ecological dimensions and through time. Measured distances along Chum Salmon (*Oncorhynchus keta*) scale radii and associated body morphology were used to construct time series of Chum Salmon growth and, by extension, time series of productivity of those ecological domains salmon have exploited. Seasonal and annual marine growth of Chum Salmon from Fish Creek, Alaska and Quilcene River, Washington were examined in relation to population abundances and climate indices, 1972–2004. Final body size at maturity of these Chum Salmon was associated with variation in immature growth incurred while in oceanic waters. Density-dependent effects and climate explained some of the variation in growth but did not account for the entire increase in size at maturity in the mid-1990s. In the Bering Sea, Chum Salmon growth was assessed as an indicator for the recruitment of Walleye Pollock (*Theragra chalcogramma*) to age-1 in an effort to

support an ecosystem-based fisheries management. Chum Salmon growth and the maximum of the monthly sea surface temperature explained 85% of the variation in age-1 Walleye Pollock recruitment. Higher Walleye Pollock recruitment success was associated with the combined effect of a cool late summer and intermediate growth of Chum Salmon. The combination of a physical and biological indicator served as the best indicators for changes in the marine growth of Chum Salmon and for the recruitment of Walleye Pollock.

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Chapter 1 General Introduction

Motivation

Development of biological time series of ocean productivity for stock assessment and recruitment forecasts for commercially important species is essential for ecosystem-based fisheries management (Marasco et al., 2007). Because marine growth of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and Bering Sea is regulated by physical, biological, and ecological processes (Kaeriyama et al., 2007; Martinson et al., 2008), their growth patterns might be used as indices of past ocean productivity. Salmon migrate over a large geographic range in the ocean, thus their marine growth is expected to reflect the influence of a composite of environmental conditions through space and time. This study evaluates seasonal and annual growth of Chum Salmon (*O. keta*) as indicators for population status and environmental and ecological variation in the North Pacific Ocean and the Bering Sea.

Specifically, I used regression and multivariate time series modeling approaches to explore the hypothesis that growth of Chum Salmon is influenced by variations in climatic and oceanic conditions and is density-dependent, and that it can be used as a biological indicator of the recruitment of age-1 Walleye Pollock (*Theragra chalcogramma*), hereafter called Pollock. For the North Pacific region (Chapter 2), scales

were collected from adult age-0.3[1] male Chum Salmon carcasses at Fish Creek near Hyder in southern southeast Alaska from 1972 to 2007 and at the Quilcence River in Washington from 1973 to 2007. The age-, sex-, and stock-specific growth of Chum Salmon was related to salmon abundance indices for the juvenile, immature, and maturing life stages to assess the changes in habitat-specific density-dependence for salmon in the North Pacific Ocean. For the eastern Bering Sea (EBS) region (Chapter 3), scale, body length, and body weight measurements were collected from Chum Salmon sampled by National Marine Fisheries Service (NMFS) observers on-board commercial fishing vessels in the EBS between 1988 and 2009. Estimated intra-annual growth in body weight of Chum Salmon, a proxy for ocean productivity, in year *t* was used as a predictor for recruitment strength, i.e., estimated abundance, of age-1 Pollock in the EBS in year *t*+1.

Scale growth and somatic growth

Growth histories of Pacific salmon are recorded on their scales. As the scale grows, concentric rings called circuli form perpendicular to the radius (Dahl, 1909). Radial growth of the scale is proportional to the growth of the fish in length (Dahl, 1909) and the incremental growth rate is represented by the distance between the circuli (Fukuwaka and Kaeriyama, 1997). Faster radial growth and more widely spaced circuli reflect growth

[1] Salmon ages are denoted *x.y* where *x* is the number of winters spent in freshwater after spending a winter in the gravel and hatching and *y* is the number of years of growth in the marine environment. Chum salmon in these populations enter the marine environment in the same year that they hatch in freshwater. Most chum salmon return as 4-year olds, but some 3-year olds and some 5-year olds are also present on the spawning grounds. An age-0.3 fish is 4 years old.

during spring and summer; narrowly spaced circuli represent growth during fall and winter (Fisher and Pearcy, 1990). In addition, the number of circuli on the scale and scale radius are both positively correlated with salmon body length (Clutter and Whitesel, 1956). In this study, the relationship between scale increments and total body size was used to estimate annual and seasonal growth in length and weight for Chum Salmon.

Scales as indicators for environmental change

The relationship between temperature and growth rate of salmon can be represented by a parabolic curve (Handeland et al., 2008). That is, there is an optimum temperature for salmon growth. In lab experiments, feeding, starvation, temperature, light, maternity, and heritability all affected salmon growth (Bilton and Robins, 1971; Bilton, 1973). Circuli in juvenile salmon formed during feeding but not during starvation (Bilton, 1973). Both the number and spacing of circuli on the scale are positively associated with feeding (Bilton, 1973). While Bilton (1973) reported that growth is more strongly affected by feeding than by temperature, it can still be concluded that the growth patterns evident on the scales of salmon can be viewed as composites of these factors (Weatherley and Gill, 1995).

Ocean growth as evidenced on the scales collected from adult salmon has been shown to correlate with physical and biological conditions in the eastern North Pacific Ocean. For Sockeye Salmon (*O. nerka*) from Karluk River on Kodiak Island, late summer juvenile growth was positively related to sea surface temperatures (SST) in the Gulf of Alaska (GOA) (Martinson, 2004), total juvenile growth increased with atmospheric circulation intensity in the eastern North Pacific Ocean, and immature

growth correlated positively with coastal precipitation (Martinson et al., 2009). For Chinook Salmon (*O. tshawytscha*) from Alaska, growth was correlated with SST, Ekman flow, and upwelling (Wells et al., 2008). In the EBS, zooplankton biomass, but not SSTs, was positively correlated with immature and maturing scale growth of age-0.2 Chum Salmon and immature scale growth of age-0.3 Chum Salmon that survived and returned to Korea from 1984 to 1998 (Seo et al., 2006). While varied, these findings consistently indicate that the growth of salmon while at sea is influenced by the interplay of a composite of environmental processes that affect ocean productivity.

Chum Salmon life history, distribution, and migration

Chum Salmon are anadromous and semelparous. Adults spawn in fresh or brackish water in rivers and lakes. In winter, fertilized eggs are incubated in interstitial spaces in gravel beds. In the spring, the fry hatch, emerge from the gravel, migrate downstream, and enter saltwater. Chum Salmon spend from a few days to several months in fresh or brackish water before entering saltwater where they rear for 3 to 6 years (Pearcy, 1992). Only during the first year at sea, salmon are referred to as juveniles, while fish in the second through penultimate year are called immatures and are referred to as maturing in their final year at sea.

North American Chum Salmon originate in rivers from as far south as the Sacramento and San Joaquin Rivers that drain into San Francisco Bay, California, and in the north to the Mackenzie River that drains into the Arctic Ocean from Canada's Northwest Territories, while Asian Chum Salmon originate from as far north and west as the Yakutsk River in the central Siberian Arctic, and along the Eastern Eurasian coast to

as far south as North Korea (Groot and Margolis, 1991). In saltwater, North America-origin Chum Salmon are primarily found east of 180° longitude and from 70°N latitude in the Chukchi and Beaufort Seas to 35°N latitude at the transition zone between the Subarctic Current and the subtropical domain in the Pacific Ocean (Quinn, 2005). Asian-origin Chum Salmon are primarily found west of 180° longitude, but overlap with North American stocks in the central North Pacific Ocean and EBS (Myers et al., 2007). While rearing in the ocean, Chum Salmon are exposed to a wide range of habitats and rearing conditions.

Chum Salmon from Oregon, Washington, British Columbia, and southeast and south central Alaska migrate on an annual counterclockwise rotation with the currents of the cyclonic North Pacific Subarctic Gyre. Juvenile North America-origin Chum Salmon from the southern extent of their range are carried northward with the northern projection of the Pacific Current. During spring and summer, these juveniles migrate above the continental shelf and counterclockwise with the Alaska Coastal Current in the GOA (Hartt and Dell, 1986; Kondzela et al., 2004). During fall, these same juvenile salmon migrate westward past Kodiak Island and enter the Alaska Stream, a fast flowing (>50 cm/s), narrow (50 km) western boundary current of the eastern Subarctic Gyre. The Alaska Stream carries them along the Aleutian Islands and into the central North Pacific Ocean and through passes in the Aleutian chain into the EBS. There they join juvenile Chum Salmon from western Alaska. The winter distribution of North America-origin juvenile Chum Salmon is unknown. Immature Chum Salmon are distributed from as far south as 40°N latitude in the North Pacific to as far north as 65°N latitude in the northern

Bering Sea and eastwards to about 170°W longitude, but are primarily found in the northeast Pacific Ocean and to the east of the Aleutian Chain (Myers et al., 2007). Maturing Chum Salmon migrate south and east to return to their river of origin or north and east for western Alaska-origin fish.

The Bering Sea is home to a mixture of Chum Salmon from Asia and North America. Juvenile Chum Salmon were mostly of western Alaskan- and Russian- origin for samples taken in the EBS in Aug-Oct 2002 (Farley et al., 2004). Yukon River fall Chum Salmon juveniles were distributed west of the Yukon River (62°N, 172°W) and south to Nunivak Island (60°N) suggesting a southwest migration along the EBS shelf (Farley et al., 2004). Kuskokwim River juvenile Chum Salmon were mostly captured south of Nunivak Island to 58°N and west to 168°W suggesting a westerly migration along the EBS shelf (Farley et al., 2004). Russian-origin juvenile Chum Salmon overlapped with western Alaska stocks as far east as 62°N, 171°W (Farley et al., 2004). Immature Chum Salmon collected in the EBS and Aleutian Islands during the fall of 2002 originated from Japan, Russia, and the United States (Kondzela et al., 2005). Genetic stock identification of Chum Salmon captured in the Pollock commercial fishery in 1994 concluded that fish originated from Asia (39-55%), western Alaska (20-35%), and southeastern Alaska, British Columbia, and Washington (21-29%) (Wilmot et al., 1998). Also the composition of Chum Salmon origin differed annually, specifically, Chum Salmon origin in 1995 was 13-51% Asian, 33-53% western Alaskan, 9-46% southeastern Alaskan, and 9-45% from British Columbia or Washington (Wilmot et al., 1998). Thus, in the EBS, juvenile salmon are primarily of western Alaskan-origin,

whereas immature and maturing salmon represent an annual changing mix of North American and Asian fish.

North Pacific Ocean

Geography

The North Pacific Ocean lies north of the Equator between eastern Asia and western North America. At 40°N to 50°N off the coast of Japan, the northward Kurishio Current collides with the southward Oyashio Current to form the west to east flowing North Pacific Current. The North Pacific Current bifurcates as it reaches North America to form the southern anticyclonic North Pacific Subtropical Gyre and the northern cyclonic North Pacific Subarctic Gyre. The GOA lies in the east and north portion of the North Pacific Subarctic Gyre, north of a line from the Alaskan Peninsula to the southeast panhandle of Alaska. The Alaska Gyre includes the northward flowing Alaska Current and westward flowing Alaska Stream off the continental shelf, and the westward flowing Alaska Coastal Current on the continental shelf.

Salmon production and climate

Over the last century, the long term abundance of salmon in the North Pacific Ocean has followed a 60 year cycle (Beamish and Bouillon, 1993). Catches of Chum Salmon, Pink Salmon (*O. gorbuscha*), and Sockeye Salmon in Japan, Russia, and Alaska were all high during the early 1930s and the early 1990s and low from the 1940s through the 1960s. These synchronous regional and species trends in catch were found to be correlated with the winter and spring atmospheric circulation pattern and intensity over the North Pacific

Ocean (Beamish and Bouillon, 1993). The increase in salmon production in the 1970s was attributed to a combination of climate-related increases in the survival of wild salmon and increases in the number of juvenile salmon released from hatcheries (Hilborn, 1992). However, these general trends do not reflect regional trends. For example, Hare et al. (1999) found that salmon catches from British Columbia to California were inversely related to overall population trends and correlated with variations in winter and spring atmospheric circulation patterns over the North Pacific Ocean.

Previous research on growth and carrying capacity

Observations of inverse relationships between body size and salmon catches have been viewed as support for the hypothesis that there is a finite carrying capacity for salmon in the North Pacific Ocean. From the mid-1970s to the mid-1990s, reductions in body size at maturity and increases in age at maturity were observed in Pink, Chum, and Sockeye Salmon from Asia and North America (Helle, 1995; Bigler et al., 1996; Helle and Hoffman, 1998). In the mid-1990s, an abrupt increase in the average size at age of salmon in combination with increased catches has been cited as evidence of an increase in carrying capacity (Helle et al., 2007). These observed variations in the size and abundance of salmon are thought to reflect temporal variation in the marine carrying capacity for salmon driven by variations in climate rather than the effects of temporal variation in management practices or changes in natal freshwater systems (Myers et al., 2001; Helle et al., 2007). However, it should be noted that from 1974 to 1991, Japan, the Republic of Korea, and Taiwan engaged in a large-scale fishery for squid in the central

North Pacific Ocean (Yatsu et al., 1993). Consequently, fishery-induced reductions in a quality prey (squid) for salmon may also have affected salmon abundance and size.

A carrying capacity for salmon in the North Pacific Ocean was inferred from inverse trends in body size and population abundance. The average size of mature salmon has also varied through time and in near synchrony across the North Pacific. The mean annual fork length of age-0.3 and age-0.4 Chum Salmon returning to rivers on the Iturup and Kunashir islands in Russia declined from 1974 to 1994, then increased from 1995 to 2004 (Kaev, 2007). From 1977 to 1990, the fork length of age-0.3 female Chum Salmon returning to 11 rivers on Hokkaido, Japan decreased by an average of 10% (Kaeriyama, 1998). For 2 Chum Salmon stock in North America, Fish Creek, Alaska, and the Quilcene River, Washington, mean annual body weights decreased by up to 46% from 1972 to 1995 (Helle, 1995; Helle and Hoffman, 1998). During the same period, Bigler et al. (1996) report that the mean annual body weight, as estimated by the biomass divided by the number of fish harvested in commercial fisheries from California to Alaska, decreased 20% in Pink Salmon, 10-24% in Chinook Salmon, 1-17% in Sockeye Salmon, and 7-31% in Coho Salmon (*O. kisutch*). Similarly, the average round weight of Coho Salmon caught in the Columbia River gillnet fishery and in the troll fishery off Vancouver Island, declined from 1974 to 1992 and increased from the 1993 to 2004 (Shaul et al., 2007). Synchronous but inverse size and abundance fluctuations in salmon populations around the Pacific Rim indicate a common factor influencing the production of salmon.

The possibility of an overall carrying capacity for salmon in the ocean was also suggested by correlative studies. For example, abundance of Sockeye Salmon during the second year at sea explained about half of the 10% to 22% decline in the average length of Sockeye Salmon returning to British Columbia and western Alaska from the mid-1950s to the mid-1970s (Peterman, 1984). Also, reductions in length and weight of Sockeye Salmon from Ozemaya River, Russia, coincided with higher returns of pink and Sockeye Salmon to the river from 1970 to 1994 (Bugaev et al., 2001). Similarly, survival and growth of Bristol Bay Sockeye Salmon from 1955 through 2000 was reduced in the second and third year at sea during years of high abundances of Asian-origin Pink Salmon (Ruggerone et al., 2003). Density-dependent effects on growth were also important in determining size at maturity in salmon (Peterman, 1984; Bugaev et al., 2001; Ruggerone et al., 2003).

Changes in the relationship between body size and abundance of salmon were also suggestive of changes in carrying capacity. The mean body weight of male and female Pink Salmon (sexes separated) was negatively related to the number of adult Pink Salmon captured in the commercial fishery along East Sakhalin, Russia, from 1958 to 1988, while average body size increased at higher Pink Salmon abundances from 1989 to 1993, suggesting that a change in the marine environment improved the carrying capacity for East Sakhalin Pink Salmon after 1989 (Nagasawa, 2000). Mean body size of Chum, Pink, and Sockeye Salmon were negatively correlated with total commercial catch of North American salmon from 1977 to 1994, but not from 1960 to 1976 (Helle et al., 2007). Increases in body size at higher production levels from 1995–2006 indicated that

the carrying capacity for anadromous salmon in the North Pacific Ocean may not be constant but instead may vary with changing physical and biological environmental conditions (Helle et al., 2007).

Mean age at maturity has also varied over time and increased in tandem with increased catches of salmon in North America and Asia. For mature Chum Salmon that returned to the Ishikari River, Hokkaido, Japan, the mean age decreased from 4.0 years to 3.5 years from 1950 to 1959 and then increased significantly from 3.5 years to 4.2 years for males and females from 1960 to 1999 (Fukuwaka et al., 2007). For male and female Chum Salmon stocks in southern southeast Alaska and Puget Sound Washington, the mean age increased from the mid-1970s to the mid-1990s (Helle and Hoffman, 1998). These findings suggest that salmon grew slower in the ocean and had to spend more time at sea to reach an optimal size for spawning when abundance was high.

Field studies of carrying capacity have included fish and oceanography surveys. Observations, statistical correlations, and linear regression models have been used to make inferences about carrying capacity in the form of inverse relationships between local density and feeding, size, and condition among individuals or groups of fish over time and space. For example, the marine survival rates of Chum Salmon and the stomach fullness of juvenile Chum Salmon was negatively correlated with the numbers of Chum Salmon fry released from the hatcheries in coastal waters of Japan (Fukuwaka and Suzuki, 2000). In contrast, in the EBS, growth of Chum Salmon was not negatively related to Pink Salmon catch per unit effort, CPUE, and it was speculated to be the results of Chum Salmon moving from the EBS to the North Pacific Ocean during years of higher

Pink Salmon abundance to avoid density-dependent reductions in growth (Azumaya and Ishida, 2000). For Chum Salmon from the EBS, a significant negative relationship was observed between CPUE of Chum Salmon and the mean growth rate for age-0.2 and age-0.3 Chum Salmon (Azumaya and Ishida, 2000). These density-dependent influences on growth were observed not only at sea but also in the returning adults.

Ecosystem models that incorporate models of zooplankton biomass are now being used to explore how carrying capacity for fish and other predators may respond to temporally varying climate and species composition scenarios (Mantua et al., 2007); for example, in the NEMURO model, changes in body size of Chum Salmon returning to Japan from the early 1970s to the late 1990s were linked to zooplankton abundances (Kishi et al., 2010), thus demonstrating the importance of these biological indices for understanding variations in salmon carrying capacities. Unfortunately, time series of zooplankton are not available for the years from the late 1990 to the mid-2000s at the time of increased body size in salmon, so that other means need to be explored to obtain measures of ocean productivity in these years.

Mechanisms linking growth to abundance

Density-dependent effects on feeding and growth of salmon support the hypothesis of a carrying capacity for these fish in the northern Pacific Ocean and the Bering Sea (Auburn and Ignell, 2000; Fukuwaka and Suzuki, 2000; Tadokoro et al., 1996). For example, stomach content weight relative to body weight of juvenile Chum Salmon in coastal waters off Japan was negatively related to CPUE of juvenile Chum Salmon in area where more than 1.7 billion Chum Salmon fry are released each year (Hiroi, 1998; Fukuwaka

and Suzuki, 2000). In the coastal waters of southern Alaska, hatcheries release over 350 million Pink and Chum Salmon fry each year (Hilborn and Eggers, 2000). An analysis of diet revealed that the diet overlap was higher for juvenile Pink and Chum Salmon (85.4% SEAK, 62.6% PWS), than for Pink and Sockeye Salmon (58.3% SEAK, 43.4% PWS), or for Chum and Sockeye Salmon (47.6% SEAK, 44.8% PWS) on the continental shelf in the GOA during 1996 (Auburn and Ignell, 2000). In the central North Pacific Ocean, Chum Salmon switched from feeding on crustaceans to gelatinous zooplankton when Pink Salmon were more abundant (Tadokoro et al., 1996). These observations of prey switching, diet overlap, and reduced feeding success at higher population levels all provide support for the hypothesis that a carrying capacity may exist for salmon in coastal waters of the North Pacific Ocean.

Previous research on growth and climate

In the last century, increases in growth of Chum Salmon were associated with conditions associated with a rise in sea temperature. For age-0.3 female Chum Salmon from the Ishikara River in Japan that reared in the Sea of Okhotsk as juveniles for years from 1967 to 1997, growth in length was negatively correlated with sea ice concentrations from 50% to 85% in the winter prior to saltwater entry and positively correlated with summer and fall SST; however the correlations between ice cover and phytoplankton biomass and between SST and zooplankton biomass were not statistically significant (Kaeriyama et al., 2007). In contrast, the juvenile scale growth of Chum Salmon returning to the Namdae River in Korea was positively correlated with zooplankton biomass in Apr, but not with sea temperatures off the east coast of Korea (Seo et al., 2006). For Chum

Salmon from Olsen Bay in Prince William Sound (1959–1975), the mean number of circuli in the first ocean zone on scales of adults age-0.3 fish was significantly and positively correlated with average summer air temperature, with fall air temperature, with summer dew point temperature, average summer and fall SSTs in the GOA, and with fall dew point temperature, and was significantly and negatively correlated with the mean percent cloud cover in the GOA (Helle, 1979). No significant correlation was found between the number of circuli and fall cloud cover, mean summer upwelling, annual upwelling, summer and fall wind speed, or the density of seawater in the GOA (Helle, 1979). For Chum Salmon from western Alaska, third-year scale growth decreased with warmer sea temperatures, while first-year scale growth increased with positive values of the North Pacific Index and reduced ice cover from 1965 to 2006 (Agler et al., 2013). Also, climate driven growth during the summer and fall of the juvenile year may be important in determining over-wintering survival (Farley and Trudel, 2009; Farley et al., 2011) and consequently merits further exploration. Generally, growth of salmon in the GOA is expected to increase with warming temperatures up to a threshold beyond which growth will be reduced.

In the lab, a nonlinear relationship has been reported between somatic growth in fish and ambient temperature (Handeland et al., 2008). This relationship is positive for low temperatures until an optimum temperature and growth rate is reached, which is then followed by a decrease in growth rates with further temperature increases. For Chum Salmon in the ocean, lethal limits for temperature are below 2.7°C and above 15.6°C, while the upper salinity limit is 34.45 (Azumaya et al., 2007). The dome-shaped

relationship is a consequence of heritable characteristics that govern metabolic efficiency and indicates that there is a species-specific optimum temperature for growth of poikilotherms (Handeland et al., 2008).

Mechanisms linking growth to climate

In the ocean, climate has direct and indirect effects on the growth of salmon. Climate variability affects growth of fish directly through the effect of temperature on metabolism and feeding efficiency (Weatherley and Gill, 1995). Salmon growth is regulated by metabolic rates at higher temperatures and by consumption rates at lower temperatures (Davis et al., 1998). *In situ*, the maximum specific growth rates (% dry wt/d) for young Sockeye Salmon occurred at lower temperatures (5°C) when fed smaller rations, while growth was most efficient at higher temperatures (15°C) when fed larger rations (Brett et al., 1969). Warmer temperatures increase metabolic demands, but also increase feeding efficiency up to a threshold. Indirectly, the influence of temperature on prey, predators, and disease can in turn influences energy available for metabolism and growth.

Eastern Bering Sea

Biogeography

The EBS is bounded in the south by the Alaska Peninsula and Aleutian Islands and to the north by the Bering Strait. This subarctic ocean is characterized by a deep basin in the southwest and a broad shallow continental shelf in the north and east. The shelf break is a focal point for primary production driven by constant upwelling of nutrients and cold water from the Aleutian Basin. Commercially important species include King

(*Paralithodes camtschaticus)*, Opilio (*Chionoecetes opilio*), and Tanner (*Chionoecetes bairdi*) Crabs, salmon, Pollock, and other groundfish (Hiatt et al., 2007). The EBS produces about half of the seafood harvested in the U.S. (FAO, 2008).

Commercial fishery for Pollock in the eastern Bering Sea

The high productivity of the EBS is expressed by a $450 million dollar-per-year and 1.4 million metric ton commercial fishery for Pollock (Hiatt et al., 2011). Pacific salmon species are captured incidentally in the fishery (Fig. 1.1 and 1.2). Specifically, Chum Salmon comprise over 99% of the non-Chinook Salmon taken as bycatch in the EBS Pollock fishery (NPFMC, 2009). From 1991 through 2012, incidental catches of non-Chinook Salmon have ranged from a low of 14,613 fish in 2008 to a peak of 697,703 fish in 2005 for the years from 1991 to 2012. The co-occurrence of Chum Salmon and Pollock provides a unique opportunity to use Chum Salmon growth as a proxy for ocean productivity to model and predict the recruitment patterns of Pollock.

Ecology of Pollock in the eastern Bering Sea

Year class strength in Pollock is largely determined at age-1, but recruitment to the commercial fishery is primarily at age-3 and higher (Ianelli et al., 2007). Annual survey estimates of the abundance of Pollock by age, including age-1 abundance, are used with fishery data in models of population dynamics to determine annual catch limits for the commercial fishery. Evidence suggests that ocean conditions in the year prior to the age-0 and age-1 life stages may affect Pollock recruitment (Quinn and Niebauer, 1995; Mueter et al., 2006). For example, in a colder summer the age-0 Pollock consumed higher energy

prey (amphipods, euphausiids, and larger copepods), had higher energy density in their bodies, and experienced a higher overwintering survival to age-1 (Andrews et al., 2009; Farley, 2009; Moss et al., 2009; Heintz and Vollenweider, 2010; Coyle et al., 2011; Heintz et al., 2013). Cooler winter temperatures were also expected to increase survival. In the lab, juvenile Pollock used 37% less energy when reared at a cooler temperature (0.5°C) than when reared at a higher temperature (2.0°C) (Kooka et al., 2007). In addition, Pollock with higher body condition factor (0.6) had lower mortality (19%), while those with lower body condition factor (0.5) had higher mortality (74.5%) (Kooka et al., 2007). A warmer subsequent spring and an early ice retreat may have led to a delayed spring bloom, elevated contemporaneous levels of zooplankton, and increases in age-1 Pollock abundances (Mueter et al., 2006). Because Pollock and Chum Salmon experience similar environmental conditions and ecological factors, observations on growth in Chum Salmon may be used to serve as a proxy for the suite of environmental and ecological factors that may affect Pollock recruitment to age-1.

Thesis statements and hypotheses

Because salmon growth depends on ocean productivity, seasonal and annual growth stanzas derived from circuli and annuli patterns on salmon scales can be used as indicators of climate variability and density-dependent effects on salmon in the North Pacific Ocean, and may also be employed as predictors of variations in the recruitment success of Pollock in the EBS. This dissertation is composed in to 2 studies reported in Chapter 2 and Chapter 3. Each chapter focuses on 1 of the 2 large marine ecosystems that

are exploited by juvenile, immature, and maturing Chum Salmon, namely the North Pacific Ocean (Chapter 2) and the EBS (Chapter 3). Findings and implications of the 2 studies are summarized and discussed in Chapter 4.

For Chapter 2, the objective was to describe how the marine growth of 2 populations of Chum Salmon—from the Quilcene River in Washington and from Fish Creek in southeast Alaska—may relate to estimates of Chum and Pink Salmon abundances in the eastern North Pacific from the early 1970s to the mid-2000s. Negative growth-abundance relationships were interpreted as evidence of density-dependent growth for Chum Salmon in the North Pacific Ocean. Because relationships between biophysical processes and variations in ocean productivity are complex and only indirectly related to growth, there was insufficient information to fully specify a mechanistic model. Instead, vector autoregression time series equations were used to jointly model climate indices and the residuals of simple regression relationships that describe Chum Salmon growth. The climate indices considered included wind velocity (an index of spring and fall phytoplankton bloom), the timing and magnitude of coastal upwelling off the Washington coast, the depth of the winter mixed layer in the GOA, summer offshore sea temperatures, and the winter Pacific Decadal Oscillation.

For Chapter 3, the objective was to examine Chum Salmon growth in year t-1 as a predictor for age-1 EBS Pollock recruitment in year t. Because the relationship between Pollock recruitment and Chum Salmon growth is moderated by variations in climate and because the form and dynamic structure of the moderating effects are latent, the relationships do not lend themselves to a known mechanistic representation. The

performance of different models of Pollock recruitment based on summer SST and various temperature composite indices was contrasted with that of models based on the growth of Chum Salmon bycatch in the B season (Jun 10–late Oct) of the EBS Pollock fishery as well as the performance of models that included SST, temperature composite indices, and Chum Salmon growth.

North Pacific Ocean

The following hypotheses were explored in Chapter 2:

Density-dependent Hypothesis: Marine growth of Chum Salmon (dependent variable) is negatively related to indices of salmon abundance (independent variable) in the Pacific Ocean, thus indicating density-dependent limitations on growth and possible carrying capacities for Chum Salmon in the Pacific Ocean.

Climate Hypothesis: Marine growth of Chum Salmon is related to various climate indices of the North Pacific Ocean listed in Table 1.1.

Bering Sea

The following hypotheses are explored in Chapter 3:

Temperature - Cool Late Summer (age-0), Cool Winter (age-0 to age-1), and Warm Spring (age-1) Hypothesis: Cooler late summer temperatures during the age-0 stage, cooler winter temperatures from the age-0 to age-1 stage, and warmer spring temperatures during the age-1 stage in year *t* may lead to higher abundances of age-1 Pollock in year *t*.

Salmon Growth - Ocean Productivity Hypothesis: Intra-annual growth in body weight estimated from total body weight, total fork length, and growth on the scale during the year of capture for Chum Salmon in year *t-1* may help predict the abundance of age-1 Pollock in the EBS in year *t*.

Expected contributions and significance of research

As part of this dissertation, I have developed and evaluated time series of life stage-specific growth of Chum Salmon in the Pacific Ocean with the goal to identify indicators for the status of this marine ecosystem, which in turn may be used to support an ecosystem-based approach to fisheries management. Variations in the stage-specific growth of these highly migratory Pacific salmon species may be viewed as a record of the influence of a vast array of habitat conditions on the fish and may therefore be interpreted as an indication of the overall status of ecological conditions in the Pacific Ocean.

Size at maturity is an important component determining the biomass of salmon available for harvest and escapement. Factors affecting final size at maturity of Chum Salmon are the results of marine growth experienced during various life stages in the ocean. Long-term changes in the marine growth of Chum Salmon have been summarized and presented for populations from Korea from 1984 to 1998 (Seo et al., 2006), Japan from 1970 to 2002 (Kaeriyama et al., 2007), Russia from 1962 to 2007 (Zavolokin et al., 2009), western Alaska from 1965 to 2006 (Agler et al., 2013), and Prince William Sound from 1959 to 1979 (Helle, 1979). Chapter 2 contributes to these studies with the addition of the analysis of time series of marine growth for 2 Chum Salmon populations from

southern southeast Alaska and Washington in the southeastern region of the Subarctic Gyre. In addition, age-specific salmon abundance indices were estimated using harvest and age composition rather than simply using lagged values of harvest. Also, estimated growth was related to climate and growth in prior years. The expected contribution was to isolate the differential influence of climate and population abundance on growth by life stage. Identifying factors affecting salmon growth allow the prediction of size at harvest in a given year.

In Chapter 3, intra-annual differences in growth of Chum Salmon in body weight will provide insight in to overall ocean productivity that is not necessarily encompassed by a specific climate index or related hypothesis (warm versus cold) and is also experienced by other commercially important species in the EBS marine ecosystem. Both biological and physical indicators were evaluated as predictors for year class strength of Pollock. Determining the early success of the year class of Pollock to age-1 may provide fishery managers with an earlier insight into the expected recruitment success 2 years in advance, thus allowing them to better advise the commercial fishery.

The ultimate goal of this research was to explore the applicability of stage-specific salmon growth estimated from scale growth data to function as a composite measure of ocean productivity, thus allowing the prediction of year class strength prior to recruitment to the fishery. Understanding factors influencing growth will provide insight into the mechanistic links between climate change and various dynamics of marine fish populations. Since salmon follow stage-specific migration patterns through the North Pacific Ocean and the Bering Sea and record their growth histories on their scales,

therefore these fish may function as mobile data loggers recording a measure of ocean productivity during their migration- and these data may be particularly valuable by allowing the early assessment of year class strength of other commercially important species, such as Pollock.

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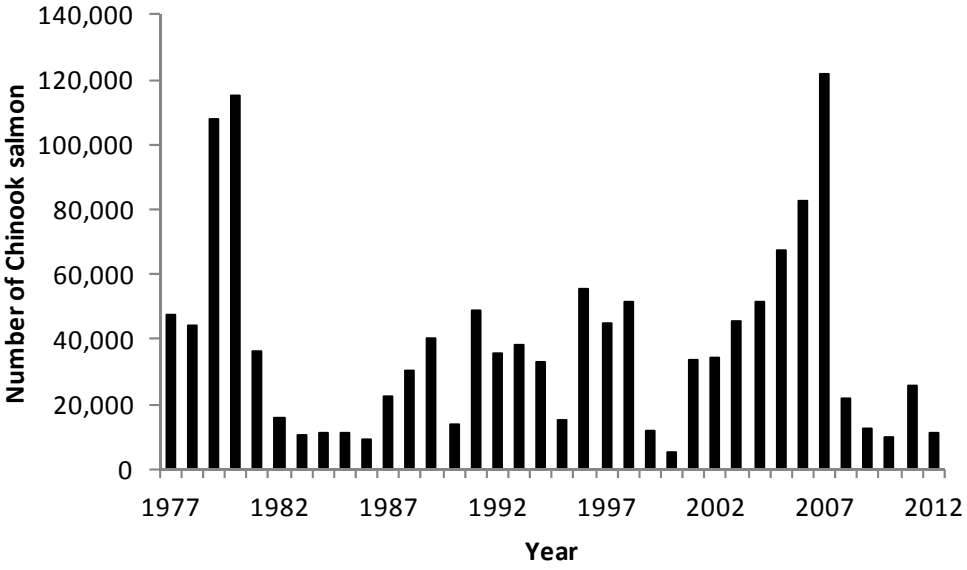

Figure 1.1 Chinook Salmon (*Oncorhynchus tshawytscha*) bycatch by Walleye Pollock (*Theragra chalcogramma*) vessels in the eastern Bering Sea. Data for 1977–90 from Queirolo et al. 1995; data from 1991–2012 from NMFS 2013a.

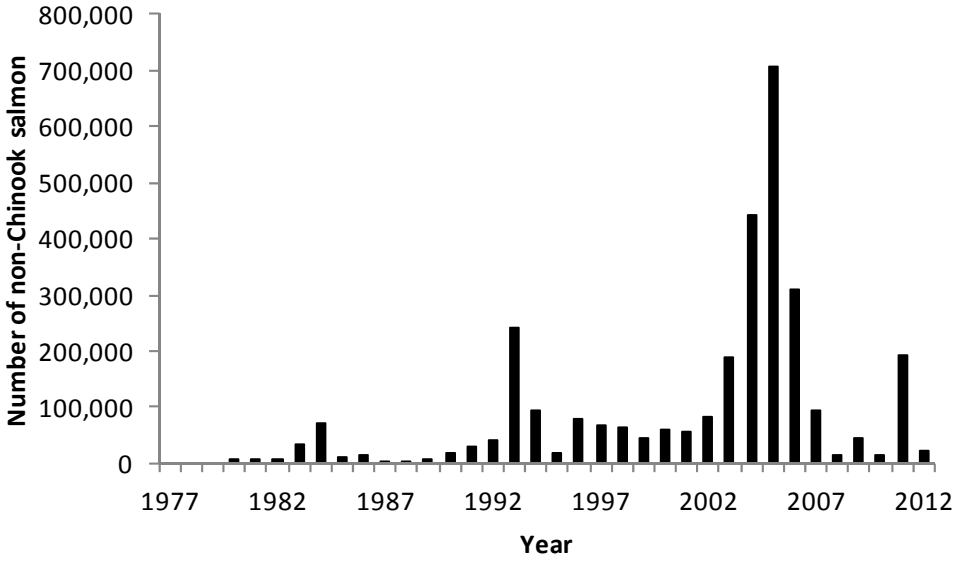

Figure 1.2 Non-Chinook Salmon bycatch by Walleye Pollock (*Theragra chalcogramma*) vessels in the eastern Bering Sea. Data for 1980–90 from Queriolo et al. 1995; data from 1991–2012 from NMFS 2013b.

Table 1.1 Mechanisms and effects for the marine growth of Chum Salmon to relate to climate indices for the North Pacific Ocean. Locations are the Gulf of Alaska (GOA), central (CNP) and eastern (ENP) North Pacific Ocean, and Washington (WA). Climate acronyms include the mixed layer depth (MLD), Pacific Decadal Oscillation (PDO), and the sea surface temperature (SST).

Stage	Location	Index	Mechanism	Effect
Fish Creek, southern southeast Alaska (saltwater entry from Feb through May)				
Early juvenile	GOA shelf	Spring wind	Plankton bloom	-
Mid-juvenile	GOA shelf	Winter MLD	Nutrients availability	+
Late juvenile	GOA shelf	Fall wind	Fall bloom	-
Immature/Maturing	CNP ENP	Winter PDO	Cool, high nutrients	+
Immature/Maturing	CNP ENP	Summer SST	Warm	+
Quilcene River, Washington (saltwater entry in May)				
Early juvenile	WA coast	Upwelling index	Nutrient upwelling	+
Early juvenile	WA coast	Spring transition	Later upwelling	-
Mid-juvenile	GOA shelf	Winter MLD	Nutrients availability	+
Late juvenile	GOA shelf	Fall wind	Plankton bloom	-
Immature/Maturing	CNP ENP	Winter PDO	Cool, high nutrients	+
Immature/Maturing	CNP ENP	Summer SST	Warm	+

Chapter 2 Growth of two Chum Salmon (*Oncorhynchus keta*) populations from southeast Alaska and Washington in relation to population abundance and climate in the eastern North Pacific Ocean, 1972–2004[3]

Abstract

Seasonal and annual marine growth of Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska and Quilcene River, Washington were examined in relation to population abundances and climate indices, 1972–2004. Growth was back-calculated using scales and lengths taken from age-0.3 male Chum Salmon carcasses. A mortality schedule, age composition, and commercial harvest data were used to back-calculate abundances of juvenile and maturing Pink Salmon (*O. gorbuscha*) and juvenile, immature, and maturing Chum Salmon from Washington and Oregon, British Columbia, southeast Alaska, southcentral Alaska, and the southern Alaska Peninsula. In linear regression models, growth was negatively related to abundance during the middle juvenile (Jul-Sep), 1st-immature, 2nd-immature, and maturing stages for the Fish Creek Chum Salmon and the 1st-immature, 2nd-immature, and maturing stages for Quilcene River Chum Salmon indicating possible density-dependent effects on growth. Juvenile and 1st-immature growth models for Fish Creek Chum Salmon and the maturing growth model for

[1]Yasumiishi, E. M., K. R. Criddle, J. H. Helle, N. Hillgruber, and F. J. Mueter. 2013. Growth of two chum salmon (*Oncorhynchus keta*) populations from southeast Alaska and Washington in relation to population abundance and climate in the eastern North Pacific Ocean, 1972–2004. Prepared for Fishery Bulletin.

Quilcene River Chum Salmon performed well in forecasting and provided insight into the effects of climate and abundance on growth of Chum Salmon from 1972 to 2004.

Introduction

Pacific salmon (*Oncorhynchus* spp.) are an important economic resource. For Asia and North America, the annual commercial harvest of salmon exceeds 4,000,000 metric tons (t) (Eggers, 2009). For Alaska, the commercial harvest of salmon in 2011 was 361,290 t with an ex-vessel value of over US $ 603 million (ADF&G, 2012). In addition to their commercial value, Pacific salmon also provide subsistence, recreation, tourism, and cultural value (NRC, 1996). Therefore, understanding factors influencing growth and size of salmon is important in understanding controls of biomass available for harvest.

The quantity of Pink Salmon (*O. gorbuscha*) and Chum Salmon (*O. keta*) available to harvest in North America has fluctuated on a multi-decadal scale over the last century (Fig. 2.1) (Eggers et al., 2005) with harvest peaks in the 1930s and the 1990s and lows in the 1950s, 1960s, and 1970s. From the mid-1970s to the mid-1990s, increases in salmon production were attributed to a combination of the effects of hatchery supplementation, increased survival of wild stocks due to favorable ocean conditions, a ban on high-seas gillnet fishery, and improved management of wild stocks (Hilborn and Eggers, 2000).

Concurrent with increases in salmon production from the mid-1970s to the mid-1980s and 1990s, reductions in the average body size and marine growth were observed in Pacific salmon from North America and Asia (Helle, 1995; Bigler et al., 1996; Helle and Hoffman, 1998; Bugaev et al., 2001; Ruggerone et al., 2003), indicating possible density-dependent effects on growth in the ocean. Based on these correlations, a hypothesis was formulated that there might be a finite carrying capacity for Pacific

salmon in the North Pacific Ocean, limited by the amount of food available to support fish growth (Helle and Hoffman, 1998). However, in the mid-1990s the body size of Chum Salmon increased during years of high salmon abundance, which might indicate interannual variation in the carrying capacity for salmon in the ocean, possibly explained by changes in the amount or composition of prey taxa.

Understanding the relationship between salmon growth and abundance is important for identifying mechanisms responsible for driving inter-annual variations in carrying capacity during a stable period (1972–2004) when body size was inversely related to abundance. This insight may help in identifying and assessing the climate influences under relatively stable management and climate regimes. Carrying capacity can be defined as the maximum biomass of a species that a specific ecosystem can support indefinitely without deterioration of the character or qualities (e.g., size and age at maturity) of the resource (Scialabba, 1998). While useful in explaining the concept, this is a rather static construct that ignores dynamic variables that might impact carrying capacity such as environmental forcing (e.g., decadal oscillations and climate change). For this study, we attempt to explore density-dependent and climate limitations on growth for different life stages of Chum Salmon by examining the effects of salmon abundance and climate on stage-specific growth of these fish in those portions of the North Pacific Ocean they occupy.

Growth of salmon is influenced by physical and biological processes. Since most fish are ectothermic, there exists a dome-shaped relationship between growth rate of fish and temperature even when they are fed *ad libidum* (Handeland et al., 2008). In the lab,

growth of salmon is influenced by population density, water temperature, light, and the quantity and quality of food (Bilton, 1973; Bilton and Robins, 1971). In the ocean, when food is not limited, salmon growth is regulated by increasing metabolic rates at higher temperatures which cannot be met with increasing consumption rates and by reduced consumption at lower temperatures (Davis et al., 1998a). Positive somatic growth is the end product of metabolism moderated by physical and biological conditions.

Somatic growth in salmon is evident in all body parts, even in the scales (Gilbert, 1913). In addition, scales have the benefit of providing a record of salmon growth by life history stage through variations in increment width (Gilbert, 1913). Thus, it is reasonable to assume that it should be possible to relate environmental variation to measures of stage-specific growth that are back-calculated from the total body length and growth taken from the scales of adult Chum Salmon.

During their marine life, Chum Salmon from Oregon (OR) to the Alaska Peninsula (AKPEN) are found primarily in the Alaska Gyre of the eastern North Pacific Ocean (Myers et al., 2007). In the first year at sea, juvenile Chum Salmon migrate with the counterclockwise Alaska Coastal Current along the Alaska coastline above the continental shelf (Hartt and Dell, 1986). At a velocity of 10 cm/s, the Alaska Coastal Current is able to transport juvenile salmon over 1000 km in about 4 months, the approximate distance from Washington (WA) to southern southeast Alaska (SSEAK) (Reed and Schumacher, 1986). During the fall, juvenile Pink and Chum Salmon migrate west and southwest along the AKPEN where they enter the swift westward flowing Alaska Stream (40 cm/s) (Reed and Schumacher, 1986). During their second through

penultimate years at sea, immature Northeast Pacific Chum Salmon are primarily distributed to the north and east of the western (160°W) and southern (50°N) boundaries of the Gulf of Alaska (GOA) in the eastern North Pacific Ocean (Myers et al., 2007). During their final year at sea, maturing salmon migrate through oceanic and continental shelf habitats to return to freshwater to spawn. Since Chum Salmon occupy different regions of the North Pacific Ocean during their ontogenetic migration from first entering the marine realm until the return to their natal streams, it should be possible to develop habitat-specific growth models that might be used to explain variations in growth at each life stage.

In this paper, the extent to which the marine growth of Chum Salmon is affected by life stage-specific population abundance was explored as an indicator of habitat-specific density-dependence and possible carrying capacities for Chum Salmon in the North Pacific Ocean. The specific objectives were to: 1) develop a model to determine the existence and magnitude of density-dependent growth during the early juvenile, middle juvenile, late juvenile, 1st-immature year, 2nd-immature year, and maturing life stages, 2) describe differences in density-dependent growth for Chum Salmon from SSEAK and WA, 3) evaluate the influence of Pink and Chum Salmon abundances on Chum Salmon growth, 4) evaluate the influence of local and regional abundances on growth, and 5) determine the influence of climate on growth. Analysis of the data relied on multiple regression and vector autoregression time series methods. The null hypothesis was that growth is not negatively related to an index of salmon abundance. That is, that salmon production was not limited by density-dependent growth in the North

Pacific Ocean. The alternative hypothesis is that growth is negatively related to salmon abundance - an indication that Chum Salmon production is limited by density-dependent growth in the North Pacific Ocean.

Mechanisms linking variation in growth to climate

The different stocks of North American Chum Salmon can be expected to be affected by different mechanisms that might have an impact on the carrying capacity of a water mass as the fish of a given life stage migrate through it. In contrast, if different life stages comingle they can be expected to be affected by similar mechanisms. Increases in growth in the eastern North Pacific Ocean are expected to be associated with increased ocean productivity due to a stronger spring bloom as indexed by reduced wind speed (Spies and Weingartner, 2007), the occurrence of a fall bloom, increased coastal upwelling, an earlier timing of spring coastal upwelling (Logerwell et al., 2003), a deeper mixing layer in the northern GOA during winter that enhances mixing of nutrients and a stronger spring bloom and enhanced summer feeding for juvenile salmon (Sarkar, 2007), warmer ocean temperatures (Martinson et al., 2008, 2009), and increased productivity offshore as indexed by the positive phase of the winter Pacific Decadal Oscillation (Mantua et al., 1997). Various mechanisms and hypothesized effects relating habitat-specific marine growth of Chum Salmon to climate indices for the North Pacific Ocean are listed in Table 2.1.

Material and Methods

Data, sample size, and assumptions

Biological data from summer Chum Salmon carcasses in Fish Creek near Hyder, Alaska in SSEAK (55°54′51″N, 130°1′28″W) were collected from 1972 to 2007 and from fall Chum Salmon carcasses from the Quilcene River and the U.S. Fish and Wildlife's Quilcene National Fish Hatchery near Quilcene, WA (47°49′55″N, 122°53′7″W) from 1973 to 2007 by the National Marine Fisheries Service, Auke Bay Laboratories in Juneau, Alaska. Fish Creek is located at the head of Portland Canal near the U.S./Canadian Border. As fry, these Chum Salmon leave their native streams in Mar through May (Heinl, 2005). Quilcene River is located on the west side of Hood Canal in Puget Sound, WA. In early May, Chum Salmon fry were released into the Quilcene River from the hatchery. The peak timing of returns to Fish Creek is in mid-Aug; returns to the Quilcene River peak in early Dec.

Scales, length, and sex data were collected from up to 300 Chum Salmon carcasses per year from both stocks. The aim was to obtain 50 samples for each sex and for the dominant age classes: age-0.2, age-0.3, and age-0.4. For this study, we only used age-0.3 male Chum Salmon to reduce variation in growth due to differences in growth between sexes and ages. Salmon ages were denoted using the decimal methods ($x.y$) where x is the number of winters spent in freshwater after spending a winter in the gravel and y is the number of winters spent in the marine environment. Body length (nearest 1.0 mm) was measured from the middle of the eye to the hypural plate (MEHP). MEHP measurements were converted to fork length (FL), i.e., the tip of the snout to fork of tail

length, by using a conversion formula from male Fish Creek Chum Salmon carcasses measured in 1974: $(FL = 1.21(MEHP) + 32.8;\ n{=}51;\ R^2{=}0.923;\ P{<}0.001)$. The FL length and measurements of the radius of the scale were used to back-calculate seasonal and annual growth. Annual sample sizes for a given stock varied from 6 to 86 scales. Years with no data included 1995, 1997 and 2001 for Fish Creek and 1980 for Quilcene River.

Scale processing and scale measurements

Growth along the radius of the scale is proportional to increases in body length in fish (Dahl, 1909). Distances between annuli on the scale represent growth from 1 year to the next and each annulus consists of multiple circuli. Circulus, and thereby annulus, spacing is correlated with somatic growth rate in salmon; widely spaced annuli (circuli) represent faster growth while more narrowly spaced annuli (circuli) represent slower growth (Fukuwaka and Kaeriyama, 1997). For juvenile Sockeye Salmon (*O. nerka*) in the ocean, absolute growth was correlated with circulus spacing and scale radius (Fukuwaka and Kaeriyama, 1997). If the total length, total scale radius, and the number of intra-annual scale increments are known, estimates of growth in length during seasons or years can be back-calculated. The averages of these growth parameters in a specified time period can then also be used to compare growth performance between time periods for specific ages, sexes, and size classes (Fukuwaka and Kaeriyama, 1997).

In this study, scales were processed for age and growth determination. In the field, scales were mounted on gum cards with the reticulated side facing up. In the lab, the reticulated side of the scales was impressed onto plastic acetate cards using a hydraulic

heated press with pressure applied for 3 minutes, at 100°C, and $3x10^4$ foot lbs (Arnold, 1951). These acetate impressions were scanned at a 24x magnification and stored in JPEG file format. The electronic images were then imported into the digitizing software program Image Pro[2] with Ringed Structure Macros developed by Media Cybernetics (Bethesda, MD). In the imaging software, a reference line was drawn from the focus to the edge of the scale along the longest axis of the anterior portion of the scale (Fig. 2.2) (Narver, 1968). A mark was placed at the end of each marine annulus to designate each annual growth zone. Scales were screened and those showing evidence of resorption or regeneration were not used in the growth analysis.

The reference line along the longest anterior axis of the scale is commonly used in growth studies on salmon (Fig. 2.2) (Martinson et al., 2008). The location of the reference line is important because it affects the number of circuli, length of the radius, number of broken circuli detected on the scale, and back-calculated estimates of growth (LaLanne, 1963; Martinson et al., 2000). In addition, designating a baseline is subject to reader bias in the interpretation of the anterior to posterior intersection; therefore, the longest axis method effectively reduces reader bias. Specifically, the Image Pro Ringed Structure macro expands a circle concentric from around the focus to a point tangent to the outer edge, which identifies the longest axis with respect to the focus.

Growth indices

Growth in length during the early juvenile, middle juvenile, late juvenile, 1st-immature,

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

2nd-immature, and maturing life stages was estimated using back-calculation methods. Each scale was measured from the center of the focus to the leading edge of the 9th circulus (*Sa*), 21st circulus (*Sb*), 1st annulus (*Sc*), 2nd annulus (*S2*), 3rd annulus (*S3*) , and to the edge of the scale (*S4*) (Fig. 2.2). Based on our measurements, the early juvenile stage represents the first 2 months at sea, namely Apr-May for Fish Creek and May-Jun for Quilcene River, the middle juvenile stage represents the next 3 months at sea, namely Jun-Aug for Fish Creek and Jul-Sep for Quilcene River, and the late juvenile stage represents growth through the end of the year as Sep-Dec for Fish Creek and Oct-Dec for Quilcene River. For each sampling location, stage-specific means for growth were calculated by year.

Linear regression models were used to relate the annual mean values of total fish length and total scale radius separately for Fish Creek and Quilcene River Chum Salmon (Fig. 2.3). The intercept in both cases was fixed at 40 mm because Chum Salmon are on average 40 mm in length at the time of initial scale formation (Kaeriyama and Bunya, 1982). Lengths at the time of complete formation of the 9th circulus (*La*), 21st circulus (*Lb*), 1st annulus (*Lc*), 2nd annulus (*L2*), and 3rd annulus (*L3*) were back-calculated using the equations for the estimated relationship between fish length and scale radius for Fish Creek Chum Salmon $Length = 40 + 228(Scale\ radius)$ and Quilcene River Chum Salmon $Length = 40 + 201(Scale\ radius)$. Annual variations in growth of the scale radius with respect to growth in length of the fish require an adjustment of the back-calculated lengths for the annual variability in the relationship between scale radius and fish length. For example, if the annual mean fish length was 10% greater than expected from the

linear regression, then fish length was assumed to be 10% greater than expected at each length increment. That is, the back-calculated lengths at each life stage were multiplied by 1.10, the ratio between the observed and expected scale radius. Growth indices were estimated from the differences in the back-calculated fish lengths: early juvenile growth, $(Ga = La)$; middle juvenile growth, $(Gb = Lb - La)$; late juvenile growth, $(Gc = Lc - Lb)$; 1st-immature year growth, $(G2 = L2 - Lc)$; 2nd-immature year growth, $(G3 = L3 - L2)$; and maturing growth, $(G4 = L4 - L3)$.

Salmon abundance indices

Salmon abundance indices for early juvenile, middle juvenile, late juvenile, 1st-immature, 2nd-immature, and maturing stages were back-calculated from time series of age composition of Chum Salmon, the numbers of Pink and Chum Salmon captured in the commercial fisheries of North America by management region and species, and marine mortality schedules for Pink and Chum Salmon. For Pink Salmon, commercial harvest can be used to index year class strength (Orsi et al., 2006; Wertheimer et al., 2011). However, the commercial harvest of Chum Salmon in a year is generally made up of multiple ages of different year classes and needs to be adjusted for marine mortality by age.

Harvest was given as the numbers of Pink and Chum Salmon captured in the commercial fisheries by management region. Commercial harvest data were available from Irvine et al. (2009) and the Statistical Yearbooks of the North Pacific Anadromous Fish Commission (www.npafc.org). We assumed that harvest was proportional to

abundance. However, catch may underestimate abundance in years when revenues are low relative to operating costs, years when runs are weak or delayed, or large and compressed in time or moderate to low and extended over longer than usual time periods.

Marine mortality rates from fry to maturity are approximately 97% for Chum and Pink Salmon (Kaeriyama, 1998). Approximately 70% of the total mortality occurs within the first 40 days at sea (Parker, 1968) with Pink Salmon experiencing a mortality of 2-4% per day (we use 3%/day) for the first 40 days and 0.4%-0.8% /day (we use 0.6%/day) thereafter. These daily mortality rates were used to develop a survival rate schedule by life stage for Pink and Chum Salmon. The product of the daily survival rates were used to expand catch to reflect abundance during the middle of each life stage in our study.

Age composition for Chum Salmon in Alaska was assumed to be well characterized by the time series of age composition from the Fish Creek stock, while the age composition for the British Columbia (BC), WA, and OR stocks was assumed to be characterized by age composition from the Quilcene River stock.

Overlap in the distribution and diets of Pink and Chum Salmon supports the approach of calculating and examining separate and combined indices for both species (Orsi et al., 2009). Maturing Pink Salmon were combined with the immature Chum Salmon because of spatial and dietary overlaps (Davis et al., 1998b), but were also analyzed separately.

The salmon abundance indices N for year t were estimated using:

$$N_t = \sum \left(p_{a,t+a} H_{a,t+a} \frac{1}{\prod S_a} \right) \quad (1)$$

where *p* was the proportion of salmon of each age class for samples taken in-river, *a* was age-class, *H* was catch, and $\prod S$ was the product of daily survival rates from the middle of the life stage being assessed to the end of life. Early juvenile, middle juvenile, late juvenile, 1st-immature, 2nd-immature, and maturing abundance indices were calculated for OR and WA (OR-WA), BC, OR-BC, OR to southeast Alaska (OR-SEAK), SEAK, SEAK to the AKPEN (SEAK-AKPEN), and OR to the AKPEN (OR-AKPEN). One additional early juvenile abundance index was calculated for SSEAK. Indices were calculated for each age and ages combined from the same brood year.

Climate indices

Six climate indices were used in this study (Fig. 2.4) including mean late spring (May-Jun) wind speed (m/s), mean fall (Sep-Oct) wind speed (m/s), deepest winter (Dec-Feb) mixed layer depth (m), spring transition index (day of year), mean summer/fall (Jul-Oct) SST (°C), and the winter (Dec-Feb) Pacific Decadal Oscillation (PDO) index. Surface wind speed data were accessed from the website for the NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Division (http://swfsc.noaa.gov/, accessed Sep 2009). Indices were derived from datasets of atmospheric pressure fields at 6 hour intervals from the Fleet Numerical Meteorology and Oceanography Center. The spring wind (WS) index was calculated as the values for Apr 16 or 17 at Dixon Entrance off southern SEAK (56.5°N, 134.5°W). The fall wind (WF) index was calculated as the average of the Sep and Oct monthly wind index values at the surface east of Kodiak Island (58.5°N, 150.0°W). A mixed layer depth (MLD) index for

winter was available for the mouth of Resurrection Bay (60°N, 149°W) in the northern GOA (Sarkar, 2007). The Freeland et al. (1997) algorithm was used to calculate the deepest winter MLD (m). The spring transition index (STI) represents the timing (day of year) of the transition from downwelling to upwelling off the coast of WA and OR (Logerwell et al., 2003). The STI values ranged from 48 in 1985 to 161 in 1993. The transition occurs between Mar and Jun. The monthly magnitude of upwelling ($m^3/s/100$ m coastline) off the coast of WA was accessed from NOAA's Pacific Fisheries Environmental Laboratory website (http://www.pfeg.noaa.gov/, accessed Sep 2008). The location of the upwelling index (UI) was 23 nautical miles (nmi) south and 13 nmi west of Cape Flattery at the tip of the Olympic peninsula off the WA coast (125°W and 48°N). A spring UI was calculated as the sum of the May and Jun indices. Sea temperature data for the eastern North Pacific Ocean was available from NOAA's Earth System Research Lab's Physical Sciences Division website (http://www.esrl.noaa.gov/psd/, accessed Apr 2012). The NCEP/NCAR reanalyzed SST dataset was used (Kalnay et al., 1996) to derive average monthly SST for a region east of 157.5°W and north of 52.4°N. Averages were computed for 3 grids of equal area (52.4°N-48.6°N x 148.1°W-157.5°W, 52.4°N-48.6°N x 148.1°W-138.7°W, and 58.1°N-52.4°N x 148.1°W-138.7°W) and then the 3 areas were averaged for each year from 1972 to 2004. An index was constructed from the average of the monthly SST from Jul 1 through Oct 31 to encompass the warmest months of the year. The PDO was calculated as the leading principle component of the Reynolds optimally interpolated monthly SST anomalies poleward of 20°N (Zhang et al., 1997). Data were available from the website of Steven Hare and Nathan Mantua at the

University of Washington, Joint Institute for the Study of the Atmosphere and Ocean (Hare and Mantua, 2000). The mean winter PDO was calculated as the average of the monthly Dec (*t*-1), Jan (*t*), and Feb (*t*) PDO values.

Growth trends

Scatter and line plots were used to assess temporal variation in the average length at maturity and growth during each life stage by stock.

Growth models

Means and standard deviations (SD) of annual means of the growth variables, abundance indices, and climate indices were calculated to provide information to interpret coefficients of the models based on normalized time series. To normalize the data, each time series was scaled and centered by subtracting the mean and dividing by the SD. This allowed interpretation of the model coefficients as the number of SDs of change in growth for each 1 SD change in the predictor variable.

Data was partitioned into 2 sets, the first for coefficient estimation and model specification and the second for model validation. The *in-sample* subset consisted of the first approximately 80% of the observations. The remaining 20% of the observations, *reserved observations,* were reserved to generate *out-of-sample* predictions using coefficients obtained for the *in-sample* model.

Two models were specified for each growth variable. Using a single generalized least squares (GLS) regression models, we described growth as a function of salmon abundance, body length at the start of the growing season, and climate index. The second

model for each growth variable relied on the iterative solution to a generalized least squares-vector autoregression (GLS/VAR) model with a simple GLS component that described growth as a function of salmon abundance and body length at the start of the growing season and a vector autoregression (VAR) process that captured dynamic variations from the lagged values of the residuals and lagged values of climate indices. GLS/VAR models were iterated until regression coefficient estimates converged. Various software programs were used in the exploration of the time series, the GLS regression modeling, and VAR modeling (Simetar, Simetar Inc., College Station, TX; Excel 2007, Microsoft Corp., Redmond, WA).

The first growth dynamic equation was a regression equation used to describe growth as a function of salmon abundance, body length at the start of the growing season and climate index. The growth dynamic equation (Eq. 2) was given as:

$$\begin{aligned} Growth_t = {} & \beta_1(Abundance_t) + \beta_2(Abundance_t)^2 + \beta_3(Length_t) \\ & + \beta_4(X_t) + \beta_5(X_t)^2 + \varepsilon_t \end{aligned} \tag{2}$$

where t was year, $Growth_t$ was a growth variable, $Abundance_t$ was a salmon abundance index (J, I, or M), $Length_t$ was body length at the start of the growing season, X_t was a climate index, and ε_t was the residual. Degrees of freedom were calculated for the generalized least squares model (n-k) from the number of observations in a time series (n) and the number of coefficients in model (k). To test for dome-shaped or asymptotic relationship between growth and abundance and climate we added a variable for the square of the abundance and climate indices.

The second growth dynamic equation was a regression equation with an error correction equation. The regression equation was used to describe growth as a function of salmon abundance and body length at the start of the growing season. The equation was given as:

$$Growth_t = \beta_1(Abundance_t) + \beta_2(Abundance_t)^2 + \beta_3(Length_t) + \varepsilon_t \quad (3)$$

where ε_t was a process that encompasses contemporaneous and serially correlated sample, observation, and model specification error. We extract signal from the noisy residuals from equation (3) using a VAR equation that relates contemporaneous values of the residuals with lagged values of the residuals and lagged values of climate indices. In a system of 2 equations, the single VAR equation for 2 variables was given as:

$$\varepsilon_t = B_{1,\varepsilon}\varepsilon_{t-1} + \ldots + B_{i,\varepsilon}\varepsilon_{t-j} + \ldots + B_{p,\varepsilon}\varepsilon_{t-p} + B_{1,x}X_{t-1} + \ldots + B_{i,x}X_{t-j} + \ldots + B_{p,x}X_{t-p} + e_t \quad (4)$$

where ε_t was a vector time series of the growth dynamic equation residuals for the 2 equations, $B_{i,j}$ are coefficients to be estimated, X_t was a vector of climate indices in time t, p was the maximal lag length, and e_t were the residuals. For the equation, the maximum likelihood estimator for the matrix coefficient B is $B = Y'Z(Z'Z)^{-1}$ where Z is a matrix composed of the elements of ε and X. Because the estimated coefficients of the VAR are conditional on the residuals of the growth model and because the estimated coefficients of the growth model are inefficient when serial correlation was present, it was necessary to iterate on equations (3) and (4) until the coefficient estimates of the growth equation converges to stable values. The degree of freedom for the GLS and VAR integrated model are (n-k-p), where p was the number of lag years. We limited the maximum lag to

4 years to account for the possible direct or indirect effect of generation cycles on growth. The Simetar software allowed us to exclude the insignificant variables in our VAR model.

For each of the 12 growth variables, we estimated a GLS model (Eq. 2) and a GLS model with an error correction (Eqs. 3 and 4) using matching dependent and independent variables for each life stage in Table 2.2. Abundance indices were added to the model separately by region and the abundances of Pink and Chum Salmon were added to the model separately and combined by region. For the immature models, single age predictors were introduced to the model beginning with the age-0.1 for the 1^{st}-immature year model and age-0.2 for the 2^{nd}-immature growth model, then additional ages were added to the abundance index to assess the influences of age-specific abundances on growth. Maturing Pink Salmon abundance was also added to each immature growth index for each region. For the maturing models, we included all ages in the model due to the similar migration path back to the continental shelf and natal regions.

A forward selection method was used with the *in-sample* observations. Each predictor was added separately to the regression models and then included in the model if significant. If predictor variables were correlated, then we retained the variable that resulted in a model with a lower Schwarz's information criterion (*SIC*). Predictor variables for equation 2 were selected based on the model with the lowest *SIC*. The abundance variable from equation 2 was then used in equation 3. The residuals from equation 3 and the climate indices were used to estimate the parameters of error

correction equation 4. Finally, we compared the *SIC*s for the GLS and the GLS model with the error correction. The best-fit GLS models and the GLS models with the error correction were tested for heteroscedasticity of the residuals (Goldfeld-Quandt, absolute residuals vs. fitted values plot), normality of the residuals (qq plots, studentized residuals vs. fitted values, and Shapiro test), serial correlation of the residuals (autocorrelation test), and multicollinearity among predictor variables (Pearson correlation). The Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test statistic was used to test for the presence of stochastic trends for the variables in the VAR models (Kwiatkowski et al., 1992). If the KPSS test rejects the null hypothesis (test-statistic > critical value), then the time series was nonstationary and a Dickey Fuller test was used to determine if the time series has a unit root. Subsequently, the time series was transformed through fractional differencing before being used in the model (Ashley and Verbrugge, 2009).

Summary statistics were compared between *in-sample* observations and estimates and *reserved observations* and corresponding estimates to validate model performance. Summary statistics used include the average, average error, mean absolute deviation, mean squared error, root mean squared error, coefficient of variation in the residuals, coefficient of determination, the *SIC*, and an *F*-test for overall model performance. An *F*-test was used to determine whether the mean squared error was significantly greater for *reserved observations* and estimates than for *in-sample* observations and estimates. If the test statistic exceeded the critical value, model performance was judged to have deteriorated over the *reserved observations*, indicative of model misspecification. Lehmann's correlation (Lehmann, 1959) was used to determine whether the mean

squared error was reduced by integrating the climate and residuals using the VAR models and for determining model performance.

Results

Trends in size and growth

Trends in annual mean body length at maturity for the age-0.3 male Chum Salmon were similar for the Fish Creek and Quilcene River stocks (Fig. 2.5). From the 1970s to the early 1990s, mean length decreased by about 11.6% (99 mm) for Fish Creek Chum Salmon (from 815 to 720 mm) and by 8.6% (60 mm) for Quilcene River Chum Salmon (from 780 to 720 mm). The decline was followed by an increase in body length in both populations, but the increase from the early 1990s to 2000 was much larger for Fish Creek Chum Salmon (9.7%) than for the Quilcene River Chum Salmon (2.8%). However, neither stock regained body lengths observed in the 1970s.

Growth trends were similar among life stages for Fish Creek Chum Salmon, but not for the Quilcene River Chum Salmon (Figs. 2.6 and 2.7). For Fish Creek Chum Salmon, the early and middle juvenile growth decreased from the 1970s to the 2000s. Similarly, the 1st-immature and 2nd-immature year growth decreased from the 1970s to the late 1980s and early 1990s, but was followed by an increase to the same growth attained in the 1970s by the year 2000. Maturing growth was higher from the 1970s to the mid-1980s, and lower from the mid-1980s to the mid-2000s. For the Quilcene River Chum Salmon, juvenile growth was variable with no trend. The 1st-immature year growth was highly variable with no trend, while the 2nd-immature year growth declined from the

mid-1970s to the late 1990s, and increased slightly in the late 1990s up to 2004.The 2nd-immature and maturing stage growth was lower in the late 1980s and early 1990s, and higher in the 1970s, early 1980s, late 1990s, and early 2000s. Between stocks, similarities in growth trends were observed for the juvenile and maturing stages. Maturing growth was higher in the 1970s and early 1980s in comparison to the mid-1990s and early 2000s.

Growth models

Averages and SDs were used to interpret the coefficients of the models (Table 2.3 and 2.4). For example, a coefficient of -0.500 (0.500) indicates a 50% decrease (increase) in 1 SD of the dependent variable (growth) with an increase of 1 SD in the predictor variable (abundance, length, or climate). We present results of the models with the lowest *SIC*, although other abundance indices may also have been significant in the models. All model residuals and climate indices used in the VAR models were stationary. Residuals of the integrated models were stationary, except for the 1st-immature year growth model for Fish Creek Chum Salmon. However, there was no evidence of a unit root process in the residuals of this model. There was no significant serial correlation in the residuals of the models.

Fish Creek Chum Salmon models

For Fish Creek Chum Salmon, growth during the middle juvenile, 1st-immature, 2nd-immature, and maturing stages were inversely related to estimates of salmon abundance in the regression models (Table 2.5, Fig. 2.8). Early juvenile growth was not correlated with climate or population abundance. Late juvenile growth was correlated

with climate. Overall, growth was reduced by 47 mm for each 1 SD increase in salmon abundance.

Middle juvenile growth was significantly and negatively correlated with the estimated abundance of juvenile Pink Salmon from SEAK to the AKPEN management region harvests and positively related to length at the start of the middle juvenile stage (Table 2.5, Fig. 2.8A). Seventy percent of the variation in middle juvenile growth was explained by length and abundance (R^2=0.700; P<0.001). Growth increased by 0.632 SD (4.1 mm) with a single SD increase in length and decreased 0.522 SD (3.7 mm) for each SD increase in abundance.

Late juvenile growth was negatively correlated with the velocity of fall winds, but not correlated with salmon abundance (Table 2.5, Fig. 2.8B). Fall winds explained 39% of the variation in growth. Growth decreased by 0.566 SD (6.8 mm) for each SD (1.2 m/s) increase in fall wind speed.

The 1st-immature year growth of Fish Creek Chum Salmon was inversely related to the combined abundances of immature age-0.1 Chum Salmon and maturing Pink Salmon based on catch data from OR to the south of the AKPEN (Table 2.5, Fig. 2.8C). The *SIC* was further reduced by including lagged values of SST, PDO, and growth in the error correction model. Growth was positively correlated with SST and growth 2 years earlier and negatively correlated with the PDO 1 and 4 years earlier. The variables in the GLS/VAR model explained an additional 46% of the variation in 1st-immature year growth in comparison to the GLS model. Growth was 1) reduced by 0.562 SD (9.0 mm) for a 1 SD increase in abundance, 2) increased by 0.405 SD (6.5 mm) when growth was 1

SD (16.0 mm) higher 2 years earlier, 3) reduced 0.533 SD (8.5 mm) and 0.216 SD (3.5 mm) with a SD (0.99) increase in the PDO 1 and 4 years earlier respectively, and 4) increased by 0.246 SD (3.9 mm) with a 1 SD (0.61°C) increase in SST 2 years earlier. Performance measures indicated reductions in the average error, mean absolute deviation, sum of squared errors, mean squared errors, root mean squared errors, and coefficients of variation when including the error correction term in the 1st-immature year growth model (Table 2.6).

The 2nd-immature year growth of Fish Creek Chum Salmon was negatively correlated with the abundance of immature age-0.2 and age-0.3 Chum Salmon and maturing Pink Salmon from OR to SEAK (Table 2.5, Fig. 2.8D). Abundance explained 32% of the variation in 2nd-immature year growth. Growth decreased 0.576 SD (7.5 mm) for each SD increase in abundance. Growth was also significantly and negatively correlated with SST, but the *SIC* was lower than for the model with abundance.

Maturing growth was inversely correlated with the abundance of maturing Pink Salmon and Chum Salmon from SEAK (R^2=0.254; P=0.007) (Table 2.5, Fig. 2.8E). The SST and the PDO were not significant in the models. Growth decreased 0.533 SD (3.2 mm) for each SD increase in abundance.

Quilcene River Chum Salmon models

Quilcene River Chum Salmon growth was inversely related to salmon abundance during the immature and maturing life stages, but not during the juvenile stage (Table 2.7, Fig. 2.9). All sets of residuals passed the test for normality, homoscedasticity, and serial

correlation. Overall, growth was reduced by 42 mm for each SD change in salmon abundance.

Contrary to expectations, middle juvenile growth was positively correlated with juvenile Pink and Chum Salmon abundances from OR to SEAK and negatively correlated with the maximum depth of the winter mixed layer in the northern GOA (R^2=0.435; P<0.001; *SIC*=150) (Table 2.7, Fig. 2.9A). Growth increased 0.560 SD (2.2 mm) for each SD increase in juvenile abundance.

The 1st-immature year growth was inversely correlated with the abundance of immature age-0.1 Chum Salmon from OR to the AKPEN. Abundance explained 28% of the variability in growth in the GLS model (R^2=0.276; P<0.001) (Table 2.7, Fig. 2.9B). The GLS/VAR model had a lower *SIC* and explained an additional 19% of the variability in growth (R^2=0.466; P<0.001). Growth was positively correlated with growth and SST 2 years earlier and negatively correlated with the PDO 2 years earlier. Growth decreased 0.471 SD (6.6 mm) for each SD increase in abundance, increased 0.386 SD (5.4 mm) for each SD (0.61°C) increase in SST 2 years earlier and decreased 0.338 SD (4.7 mm) for each SD (1.0) increase in the PDO 2 years earlier. Performance measures indicated reductions in the average error, mean absolute deviation, sum of squared errors, mean squared errors, root mean squared errors, coefficients of variation and *SIC* for the 1st-immature model and 2nd-immature model with the error correction term (Table 2.8).

The 2nd-immature year growth was inversely correlated with the abundance of maturing Pink Salmon and immature age-0.1, age-0.2, and age-0.3 Chum Salmon from OR to AKPEN (R^2=0.572; P<0.001) (Table 2.7, Fig. 2.9C). The GLS/VAR model

explained an additional 23% in growth (R^2=0.802; P<0.001) and reduced the *SIC*. Similar to the 1st-immature year growth models for both stocks, growth was positively correlated with SST 2 years earlier and negatively correlated with the PDO 2 years earlier. Growth decreased 0.777 SD (8.5 mm) for each SD increase in abundance, decreased 0.352 SD (3.9 mm) for each SD increase in growth 4 years earlier, increased 0.309 SD (3.4 mm) for each SD (0.61°C) increase in SST 2 years earlier and decreased by 0.442 SD (4.9 mm) for each SD (1.0) increase in the winter PDO 2 years earlier.

Maturing growth was negatively correlated with the abundance of maturing Pink Salmon and Chum Salmon from OR to SEAK (R^2=0.355; P<0.001) (Table 2.7, Fig. 2.9D). Each 1 SD increase in abundance resulted in a 0.608 SD (7.9 mm) reduction in growth. Maturing growth was not correlated with the climate indices in this study.

For the *reserved observations*, the growth models that performed as well or better than the *in-sample* in forecasting included the juvenile and maturing models for Fish Creek and maturing model for Quilcene River Chum Salmon (Tables 2.9 and 2.10). Negative R^2 values indicate that the mean of the growth time series performed better in forecasting than the fitted values for the immature GLS models for the Fish Creek Chum Salmon and for the juvenile and immature models for Quilcene River. Significant model deterioration occurred for the immature Fish Creek models and the juvenile and immature models for the Quilcene River Chum Salmon as indicated by the *F*-statistic for model deterioration (*F*-det.). Although the 1st-immature Fish Creek GLS/VAR integrated model performance deteriorated when fit to the *reserved sample*, the model still explained 44% of the variation in growth compared to the negative coefficient of determination of the

GLS model. The maturing growth model did not deteriorate, but the coefficient of determination was close to zero.

According to the results of the Lehmann's correlation test (Table 2.11), the mean squared errors were significantly reduced for 2 of 3 *in-sample* regression equations when integrating the error correction equation. The mean squared errors were significantly reduced for the 1st-immature Fish Creek and 2nd-immature Quilcene River models, but not the 1st-immature Quilcene River model. However, the mean squared error was not significantly reduced for any model when applied to the *reserved observations*.

Discussion

This research provides insight into factors that affect growth of Chum Salmon for different life stages of 2 geographically separated stocks in the eastern North Pacific Ocean. We found evidence for density-dependent growth during the juvenile, immature, and maturing life stages. When testing the models using the *reserved observations*, the models fit the growth data well for the juvenile, 1st-immature, and maturing models for Chum Salmon from Fish Creek, SEAK, and for the maturing models for Chum Salmon from the Quilcene River, WA.

Trends in size and growth

Size at maturity is important in determining fecundity, breeding success, and survival of progeny in salmon (Helle, 1979; 1989; Schroder, 1982). Therefore, it is essential to understand factors influencing growth. Large-bodied female salmon can dig deeper redds (van de Berghe and Gross, 1984), produce more eggs (Helle, 1989), produce larger eggs

and fry (Koski, 1975), and have progeny with higher survival probability (Helle, 1979; 1989). Larger males are more aggressive and are more successful in competing for a mate than smaller males (Schroder, 1982). In the ocean, larger salmon consume more prey, more energy-rich prey, and more diverse prey than smaller salmon (Davis et al., 2009) indicating a competitive advantage for larger fish. Since a growth advantage once gained has a high likelihood of being maintained throughout the fish's life, these factors highlight the significance of understanding the impacts of climate and population abundance on the marine growth and ultimately the size at maturity of salmon.

In this study, we demonstrated that declines in the body size at maturity from the early 1970s to early 1990s were associated with decreases in early juvenile, middle juvenile, immature, and maturing growth for Fish Creek Chum Salmon and to decreases in the immature and maturing growth for Quilcene River Chum Salmon. Our results are comparable to observed declines in body size of Hokkaido Chum Salmon in the mid-1980 that were associated with reduced growth during the 2nd-immature and maturing stages for years 1970–1994 (Kaeriyama, 1998). Similarly, the reduction in the adult (mature) body size of Chum Salmon from the Anadyr River in Russia during the mid-1980s was associated with reduced growth in the immature and maturing stages (Zavolokin et al., 2009). Although the general trends in size at maturity from the 1970s to the 1990s were similar for different populations around the Pacific Ocean, the changes in adult size were associated with different developmental stages, namely the immature and maturing life stages in the western Pacific and the juvenile, immature, and maturing life stages in the eastern Pacific.

Juvenile and maturing growth of Chum Salmon from the 2 populations in our study did not recover from the size reductions from the early 1970s to the early 1990s. Conversely, juvenile Chum Salmon released from Japan into the Sea of Okhotsk had lower growth from the late 1960s to the mid-1980s and higher growth from the mid-1980s to the mid-1990s, possibly due to reduced ice cover and warmer sea temperatures during summer and fall (Kaeriyama et al., 2007). Farther north in Russia, juvenile growth of Chum Salmon departing the Anadyr River was relatively stable from the early 1960s to the late 2000s, but slightly higher in the late 1990s (Zavolokin et al., 2009). The difference in the patterns in juvenile growth of Chum Salmon between the eastern and western Pacific Ocean populations indicates that conditions in the 1990s were more favorable for juvenile Chum Salmon in the western North Pacific than the eastern North Pacific Ocean. Declines in zooplankton biomasses were documented in both regions of the North Pacific Ocean from the mid-1970s to the early 1990s, but remained 50% to 300% higher in the western North Pacific (Sugimoto and Tadokoro, 1997). In 2005, the condition factor and diversity of prey were significantly higher for Chum Salmon in the western Subarctic Gyre along 165°E longitude than for Chum Salmon in the western GOA along 165°W longitude (Sagawa et al., 2007). Lower ocean productivity in the eastern Pacific may account for the lower juvenile growth of the 2 Chum Salmon populations in our study during the 1980s and 1990s.

In this study, increases in size at maturity in the 1990s were associated with increases in immature growth. However, in the forecasts our models did not capture the entire increase in the 1st- and 2nd-immature years of growth for Fish Creek and Quilcene

River Chum Salmon. Alternative mechanisms may exist that can explain the increase in immature growth in the mid-1990s. For example, the annual growth during age-0.1, -0.2, and -0.3 immature stages measured on the scales of adult Chum Salmon from Korea was positively correlated with zooplankton biomass in the Bering Sea (Seo et al., 2006), thus establishing a potential pathway for climate-induced changes in growth. Helle and Fukuwaka (2009) found a strong positive correlation between body size of maturing Chum Salmon from the eastern North Pacific and Japan and the spring and summer sea temperatures in the southeastern Bering Sea for the period 1977–1994, but weak and often negative correlations during 1960–1976 and 1995–2006 period. Additional factors, such as zooplankton biomass and prey diversity, need to be investigated to determine the cause of increases in size in the mid-1990s.

Growth and abundance

Evidence of density-dependent growth was detected for the juvenile Chum Salmon from Fish Creek, but not for those from Quilcene River. One explanation for this discrepancy in growth patterns might have been the much higher abundance of Pink and Chum Salmon in SEAK in comparison to WA and OR. In fact since 1995, the harvest of pink and Chum Salmon has been 5 to 12 times higher in the GOA region than in WA, OR, and BC combined (Eggers et al., 2005). Annually, Alaska hatcheries release approximately 1.5 billion juvenile salmon into the Pacific Ocean (ADF&G, 2012) and the primary species released are Pink and Chum Salmon. Pink Salmon are primarily released from Prince William Sound hatcheries, while Chum Salmon are the primary species released from hatcheries in SEAK. In the waters off Japan, where hatcheries along the Sea of

Honshu release 100-300 million juvenile Chum Salmon annually, the relative weight of stomach contents of juvenile Chum Salmon contents decreased as their density increased, which was postulated to be the result of juvenile Chum Salmon depleting prey abundances (Fukuwaka and Suzuki, 2000). Similarly, early marine growth of Atlantic Salmon (*Salmo salar*) from the Miramichi River in eastern Canada was inversely related to subsequent recruitment (Friedland et al., 2009). To validate our findings with other observational data, we examined the mean body length of juvenile Chum Salmon and the surface trawl catch of juvenile Pink and Chum Salmon from continental shelf waters off Icy Point in the GOA from 1997 to 2011 (courtesy of the SEAK Coastal Monitoring Program, Alaska Fisheries Sciences Center, Juneau, Alaska); at the station with the highest annual catch of juvenile Pink and Chum Salmon, we found an inverse relationship between the inter-annual mean length of Chum Salmon and catch of juvenile Pink and Chum Salmon in tows with more than 250 fish, possibly indicating a threshold abundance for density-dependent effects. However, these fish were the size of our fish during the early juvenile stage and may not represent processes affecting mid-juvenile growth later in life while in the GOA.

Differences in the influence of Pink Salmon population abundances on growth of the 1st-immature stage of Chum Salmon from the 2 populations investigated may be the result of differences in the migration and distribution of age-0.1 Chum Salmon. The 1st-immature year growth of Fish Creek Chum Salmon was inversely related to the abundance of maturing Pink Salmon and age-0.1 Chum Salmon, while Quilcene River Chum Salmon were more significantly correlated with the abundance of immature

age-0.1 Chum Salmon. Chum Salmon from WA and SEAK reside primarily in the eastern North Pacific and GOA (Urawa et al., 2009). However, 70% of the age-0.1 Chum Salmon along the 145°E longitude from 48°N to 53°N were of SEAK origin and less than 1% of WA origin during Feb (Beacham et al., 2009). Pink Salmon are more abundant farther north in Prince William Sound than in SEAK or WA. That is, the southern-origin Chum Salmon were not likely distributed as far west or north as their northern conspecifics at age-0.1.

Density-dependent effects were greater on growth in the 2nd-immature stage for the Quilcene River Chum Salmon than the Fish Creek Chum Salmon as indicated by the larger magnitude of the negative coefficient for salmon abundance. By the 2nd-immature and maturing stages, Quilcene River Chum Salmon are smaller than those from Fish Creek and may therefore be more vulnerable to the effects of higher population abundance on growth. It has been observed that larger Chum Salmon consume higher quality prey than smaller fish (Davis et al., 2009); thus, in areas of overlap Quilcene River Chum Salmon may be at a competitive disadvantage relative to larger Chum Salmon from other regions. In addition, Quilcene River Chum Salmon may distribute in regions of lower productivity or higher population density. Moreover, run timing may also influence the density-dependent growth of these 2 stocks; e.g., summer-run Chum Salmon from Fish Creek leave freshwater from Feb through Mar and return to freshwater in Aug, while Quilcene River Chum Salmon leave freshwater in May and return to freshwater in Dec (Heinl et al., 2000). Consequently, migration timing of Fish Creek Chum Salmon matches the timing of Pink Salmon migration, whereas Quilcene River

Chum Salmon leave and return to the freshwater later in the year. To address differences in the migration routes of summer and fall Chum Salmon a comparison of the marine growth could be made between summer and fall Chum Salmon from the same river or area.

Pink Salmon abundance consistently influenced the growth of both populations of Chum Salmon, except in the 1st-immature year of Quilcene River Chum Salmon. This observation is not surprising because Pink Salmon are the most abundant North American species of Pacific salmon (Eggers et al., 2005). However, Chum Salmon mature at multiple ages within a brood and are likely more abundant as immatures than the maturing Pink Salmon. Other studies document the effects of Pink Salmon abundance on the feeding of Chum Salmon. In odd-years of higher Pink Salmon abundances in the ocean, Chum Salmon were observed to consume less prey (Ivankov and Andreyev, 1971; Salo, 1991), shift their diet to less nutritious prey (Salo, 1991), and switch from eating crustacean zooplankton to eating gelatinous zooplankton (Tadokoro et al., 1996). From these studies it appears that the influence of Pink Salmon abundance may be greater than that of Chum Salmon due to their high population levels, fast growth rates, high degree of diet overlap with other salmon species, as well as their preference for lower trophic level prey, and their early migration to sea (Ruggerone and Nielsen, 2004).

Chum Salmon growth was more strongly correlated with local abundances than regional abundances during the juvenile and maturing stages, but more correlated with regional abundances during the immature life stages. Other studies have examined the influences of local and regional population abundances on the growth of Chum Salmon.

For example, the average distances between the circuli on the scales of adult age-0.2 and age-0.3 Chum Salmon from the Anadyr River, Russia, from 1962 to 2007 were negatively correlated with the total catch of Pacific salmon in the Pacific Ocean during the immature and maturing stages, but not during the juvenile stage (Zavolokin et al., 2009). Also, trends in growth of western Alaska Chum Salmon were more similar for adjacent rivers than for more widely separated rivers (Agler et al., 2013). Similarly, for North American stocks of Chum Salmon there was a stronger positive covariation in the spawner-to-recruit survival rates between neighboring stocks than for more widely separated stocks and only little evidence of covariation between stocks originating more than 1000 km apart (Pyper et al., 2002). One explanation for this observation may be that while Pacific salmon distribute as immatures within a mixture of stocks on the high-seas, they are more likely to have stock-specific migration pathways while leaving and returning to coastal waters as juveniles and as maturing fish. Consequently, they may be experiencing similar environmental forcing which may lead to similar growth patterns among local populations and may therefore lead to similar survival rates.

Several direct and indirect mechanisms exist for salmon to compete for resources in the ocean, particularly because the different species of Pacific salmon have a high degree of overlap in prey and habitat (Myers et al., 2007). Physical and biological conditions in the marine environment have direct and indirect influences on density-dependent growth through their influences on feeding and metabolic rates (Davis et al., 1998a). In salmon, behavioral responses to competition or interference include reduced feeding, prey switching, and migration to alternate habitats in the ocean (Azumaya and

Ishida, 2000; Davis et al., 2009). In addition to direct interaction, there may also be indirect density-dependent interactions among Pink and Chum Salmon that could affect growth of Chum Salmon. For example, while the density of Pink Salmon was higher in odd-numbered years in the Bering Sea, the growth of Chum Salmon was also higher (Azumaya and Ishida, 2000). This may be explained by the observation that in odd-years, Chum Salmon are more likely to move from the Bering Sea to the eastern North Pacific Ocean to avoid interaction with Asian-origin Pink Salmon (Azumaya and Ishida, 2000). In the eastern North Pacific Ocean, Chum Salmon were more abundant and consumed lower quality prey (gelatinous zooplankton) in odd-numbered years, whereas in even-numbered years Chum Salmon abundance was lower and they consumed higher quality prey (squid and fish; Tadokoro et al., 1996), suggesting an indirect effect of Pink Salmon abundance in the Bering Sea on the intra-specific competition of Chum Salmon in the eastern North Pacific Ocean. The ability of Chum Salmon to display plasticity in migration and feeding patterns may also be an adaptive response to more effectively reduce the impact of density on growth.

Growth and climate

Contrary to our hypotheses, a shallower mixed layer depth in the previous winter at the inner continental shelf of the northern GOA was associated with an increase in growth, but only for Quilcene River Chum Salmon. During winter, nutrients from near the bottom are mixed into the water column by winds. In addition, the deeper winter mixing and strong coastal downwelling during winter may also aid to transport nutrients from coastal to offshore water (Weingartner et al., 2002). However, an early and stronger stratification

in spring favors primary production in the middle shelf of the GOA (Henson, 2007). As a result, year class strength of hatchery Pink Salmon from Prince William Sound was positively correlated with spring water column stability in the Sound, but not in the inner or middle shelf waters of the GOA (Miller at al., 2012). Therefore, we would expect that water column stability during spring rather than a deeper mixing in winter would favor Chum Salmon growth.

As anticipated, a fall phytoplankton bloom, which is generally followed by a peak in secondary productivity, as indexed by lower wind speed in Sep and Oct, was associated with an increase in the late juvenile growth of Fish Creek Chum Salmon. However, the index was not correlated with late juvenile growth of Quilcene River Chum Salmon. These fish may distribute more westward in the southern GOA rather than in the northern GOA. In the GOA, a fall bloom can occur during Sep and Oct, but does not occur every year (Cooney, 2005). The fall bloom is initiated when fall winds deepen the mixed layer and resupply nutrients to the photic zone. Once nutrients are added to surface waters, a stratification of the water column is required before a fall bloom can occur (Cooney, 2005). Thus, a fall bloom is only possible in those years, when wind speeds in Sep and Oct are not excessive.

Cooler late summer and fall SSTs were associated with an increase in growth during the 2nd-immature stage for the Fish Creek Chum Salmon, but growth was more strongly correlated with population abundance. Immature growth of western Alaska Chum Salmon was negatively correlated with GOA SSTs 1965 to 2006 (Agler et al., 2013). This pattern might be explained by the fact that salmon in the eastern Pacific

Ocean and eastern Bering Sea are consuming higher quality prey in cool years (Aydin et al., 2000; Coyle et al., 2011). Specifically, in the eastern Bering Sea, Chum Salmon consumed primarily euphausiids in cold years and Walleye Pollock (*Theragra chalcogramma*) in warm years (Coyle et al., 2011). Similarly, during the cold years 1996 and 1998, Chum Salmon were larger and their diets consisted of proportionately more Gonatid Squid (*Berryteuthis anonychus*) (Aydin et al., 2000) in comparison to the 1997 warm year. In addition to the effect of rearing temperature on zooplankton, it was also suggested that differences in diet and growth of Chum Salmon might have been the result of interannual variations in the latitudinal position of the Subarctic Current in the North Pacific Ocean.

After accounting for density-dependent affects, growth was positively related to SST. Different possible mechanisms exist for immature growth to increase with warmer summer SSTs and negative PDO events in earlier years. For example, different physical phenomena (e.g., eddies, wind patterns, El Nino events) may transport nutrients into oceanic water of the North Pacific Ocean. Predominant among them are eddies, which form in waters above the continental shelf and slope in the eastern North Pacific Ocean (Ladd et al., 2005). In the cores of these eddies, iron and nitrate are transported from the sea floor to surface waters (Johnson et al., 2005) and these nutrients may result in phytoplankton blooms inside the eddies as they move into oceanic waters (Ladd, 2007). Zooplankton species are similarly transported from the shelf into the GOA (Mackas and Galbraith, 2002a). These eddies form more frequently in warmer years and during El Nino events (Crawford and Whitney, 1999). In a winter with a negative PDO, there is a

northerly wind pattern in the eastern North Pacific (Mantua et al., 1997) and these winds may push these eddies off the shelf and into oceanic waters. In addition to the effect of eddies on the productivity of oceanic waters, El Nino events can lead to a transport of heat and zooplankton from the Equator and these waters can reach the subarctic waters of the North Pacific Ocean in 1 to 2 years (Peterson et al., 2002; Mackas and Galbraith, 2002b). These events of increased ocean productivity may initiate and perpetuate a strong year class of a given prey taxon with a 2-year life-span. Finally, climate may also have a lag effect on growth through the lag effects of climate on mortality, predation, competition, and recruitment that influences growth, abundance, or the growth/abundance relationship. Uncertainties in regard to the true mechanisms driving the annual variation in the growth of Chum Salmon support the use of an error correction time series model.

No climate-related changes in growth were detected during the maturing life stage of either stock. This may be explained by the fact that during this stage, salmon growth favors an increase in body weight rather than length (Aydin et al., 2000), making it impossible for our length-based models to capture changes in growth. Thus, our index of growth in length may not capture the total effects of climate or population abundance on growth. Alternatively, at larger body sizes, Chum Salmon switch from feeding on zooplankton to feeding on fish and gelatinous zooplankton not used by the other salmon species (Davis et al., 2009). This feeding plasticity may reduce the effects of intra- and inter-specific competition for the larger, maturing Chum Salmon.

Study caveats

The model with the error correction that incorporated the lag structures of the model residuals and climate did a relatively good job of predicting the values of the *reserved observations* for the 1st-immature growth of the Fish Creek Chum Salmon, but a poor job for the immature growth of the Quilcene River Chum Salmon. The error correction component may have been incorrectly specified, the growth and abundance relationships may have undergone temporal change, or the time series may have been too variable or too short to provide reliable coefficient estimates. The error correction did not account for the total increase in growth in the late 1990s and early 2000s. Helle et al. (2007) suggested that the increase in body size of Chum Salmon in the mid-1990s during a period of high population abundance was due to an increase in the carrying capacity for salmon in the North Pacific Ocean. This question merits further investigation.

While uncertainty exists whether back-calculated abundance indices that are based on the numbers of returning salmon, age composition, and marine mortality are good indices for abundance earlier in life, this assumption is confirmed by a strong correlation between the abundances of juvenile Pink Salmon and the returns of adult Pink Salmon in the following year (Orsi et al., 2009). Nonetheless, it would have been preferable to base this analysis on time series of actual abundance data of juvenile and immature salmon at sea. This, however, is currently impossible, since very few such time series exist and all of those are too short to be effectively used for this study. In addition, at-sea estimates of abundance are likely subject to large sampling uncertainty, hence

indices based on harvest data, age composition, and assumed mortality rates may actually represent a better alternative.

Study advances

Our study advances the understanding of factors influencing marine growth of Chum Salmon in the North Pacific Ocean and the eastern Bering Sea. With this study, we contributed 2 more Chum Salmon populations, 1 from the SEAK and 1 WA to a growing body of growth studies on populations from southcentral Alaska (Helle, 1979), western Alaska (Agler et al., 2013), Russia (Zavolokin et al., 2009), Japan (Kaeriyama et al., 2007), and Korea (Seo et al., 2006). Contrary to the Asian populations, we found that juvenile and maturing growth did not increase in the mid-1990s indicating that productivity on the continental shelf in the east remained relatively lower than in the western Pacific Ocean. In addition, this was the first study to back-calculate indices of salmon abundance using harvest data, age composition, and mortality schedules; therefore, this index is more likely to accurately represent the actual abundances of Chum Salmon than estimates based on harvest alone. We found that size of the adult fish was related to growth in oceanic waters during the immature life stage and that immature growth was related to population abundance and to climate in prior years. Further research needs to focus on identifying and better understanding factors influencing immature growth in order to allow more accurate predictions of size at maturity for returning Chum Salmon in a given year.

Implications for management

During the first year at sea, size is considered a critical factor affecting marine mortality rates of salmon (Parker, 1971; Holtby et al., 1990). Size attained by the first winter at sea is also considered important in determining brood strength (Beamish and Mahnken, 2001). We found that an increase in the abundance of juvenile Pink Salmon from SEAK has the potential to reduce growth of Fish Creek Chum Salmon. Therefore, fishery and hatchery managers may consider adjusting the number of Pink Salmon fry released from hatcheries into coastal waters in order to increase early growth and subsequent survival of juvenile Chum Salmon.

Climate during the 1st year at sea is strongly correlated with survival in salmon (Mueter et al., 2002; Martinson et al., 2009). We found that the late juvenile growth of Chum Salmon from Fish Creek increased as the velocity of surface winds decreased in the fall, an indicator for the occurrence of a fall phytoplankton bloom. Therefore, the wind velocity index in the northern GOA may be a useful predictor for the marine survival of Chum Salmon from the GOA.

Conclusions

Scales are a valuable tool for assessing changes in the productivity of nearshore and oceanic environments in the ocean. Scale patterns contain records of integrated environmental conditions that influence the size at maturity of adult salmon returning to their natal streams. Further investigation is needed to identify important factors affecting the immature growth of Chum Salmon in offshore waters in order to better understand factors affecting the increases in the size of adults in the mid-1990s. Most importantly,

this study illustrates the importance of maintaining long-term monitoring projects. Scales consistently collected from specific stocks represent a valuable data source for assessing the influence of habitat-specific environmental factors on the productivity of commercially important fish species in marine ecosystems.

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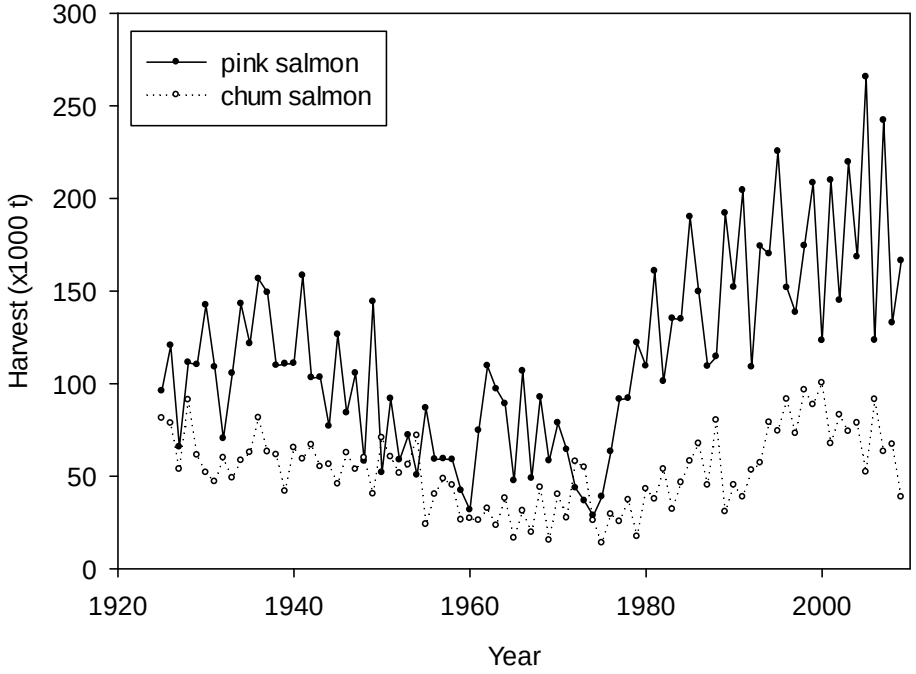

Figure 2.1 Pink (*Oncorhynchus gorbuscha*) and Chum Salmon (*Oncorhynchus keta*) captured in the commercial fisheries of the eastern North Pacific Ocean. Data are from Eggers et al. (2005) for years from 1925 to 2003 and from the North Pacific Anadromous Fish Commission Statistical Yearbooks for years from 2004 to 2009 (www.npafc.org).

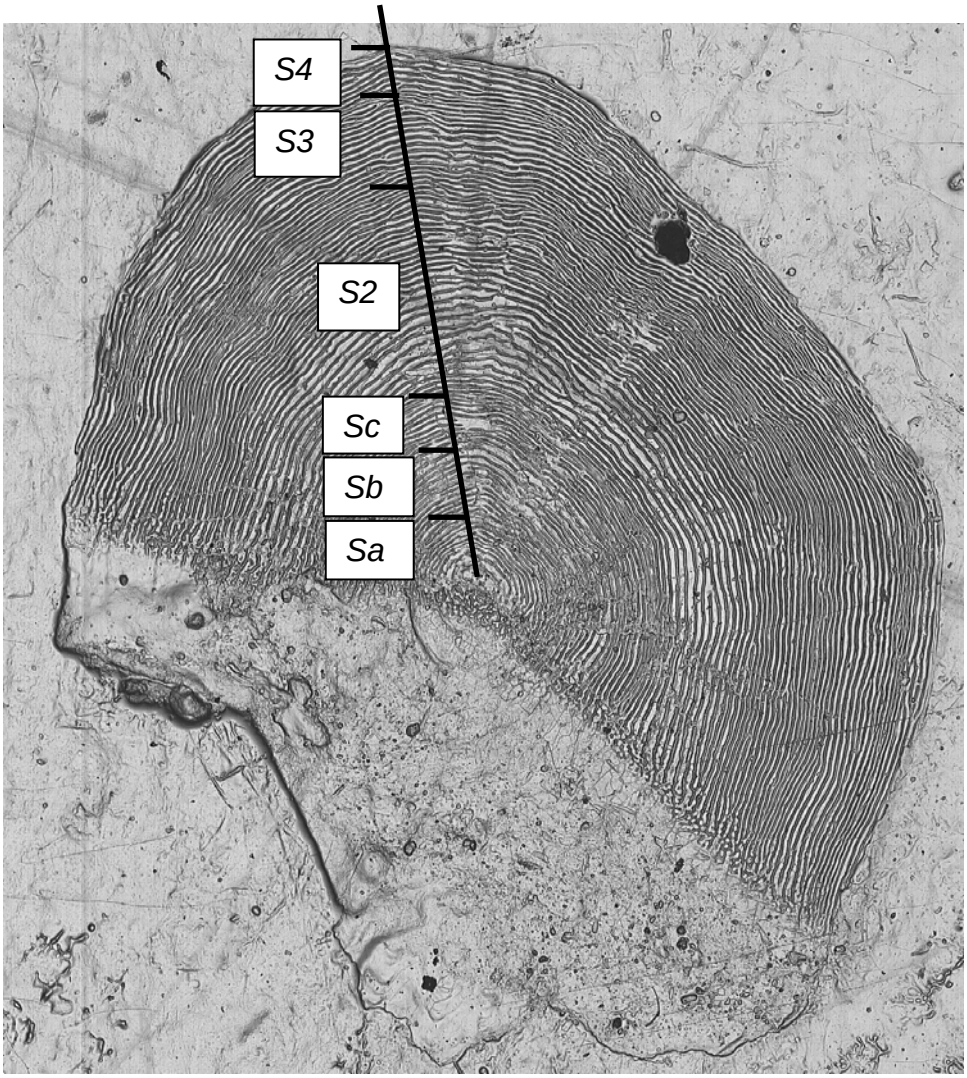

Figure 2.2 Scale image from an age-0.3 Chum Salmon (*Oncorhynchus keta*) showing the longest axis reference line used for collecting growth and radius measurements for the early (*Sa*), middle (*Sb*) and late (*Sc*) juveniles, 1st-immature (*S2*), 2nd-immature (*S3*), and maturing (*S4*) stages.

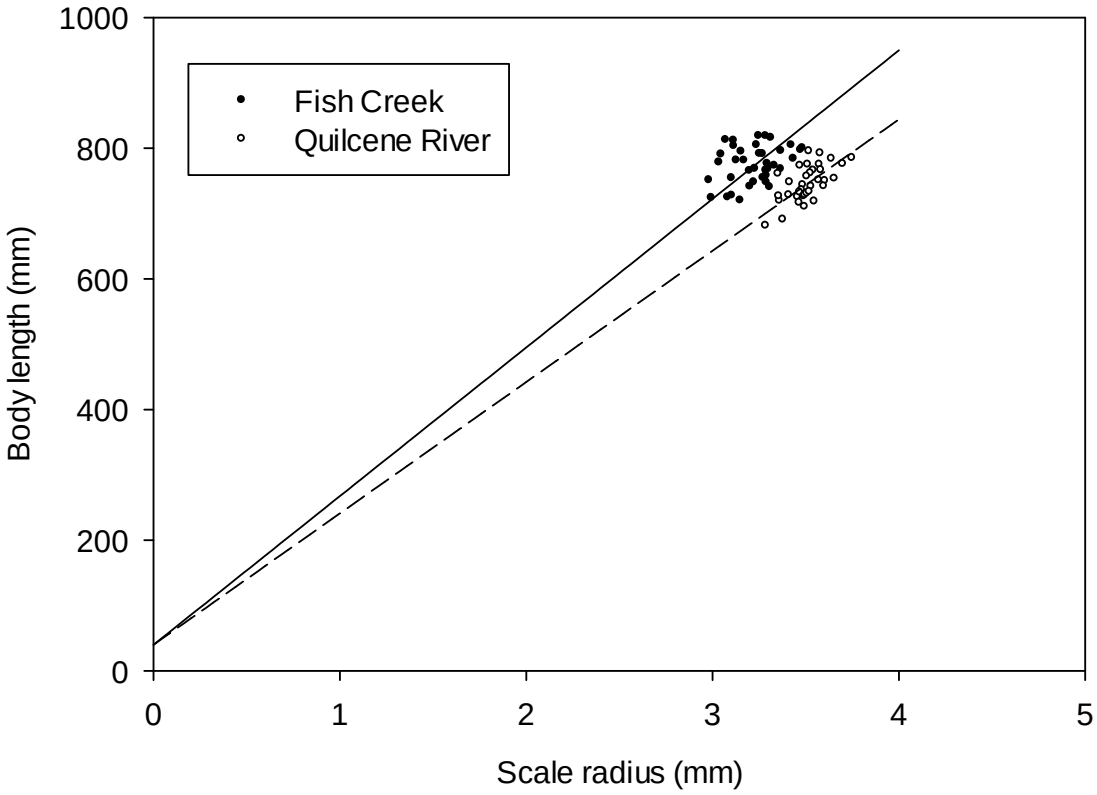

Figure 2.3 Relationship between the fish length and scale radius annual averages fit through the y-axis at 40 mm for Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska (solid line) from 1972 to 2009 (missing years: 1995, 1997, 2001, and 2008) and Quilcene River, Washington (dashed line) from 1973 to 2007 (missing years: 1980 and 2005).

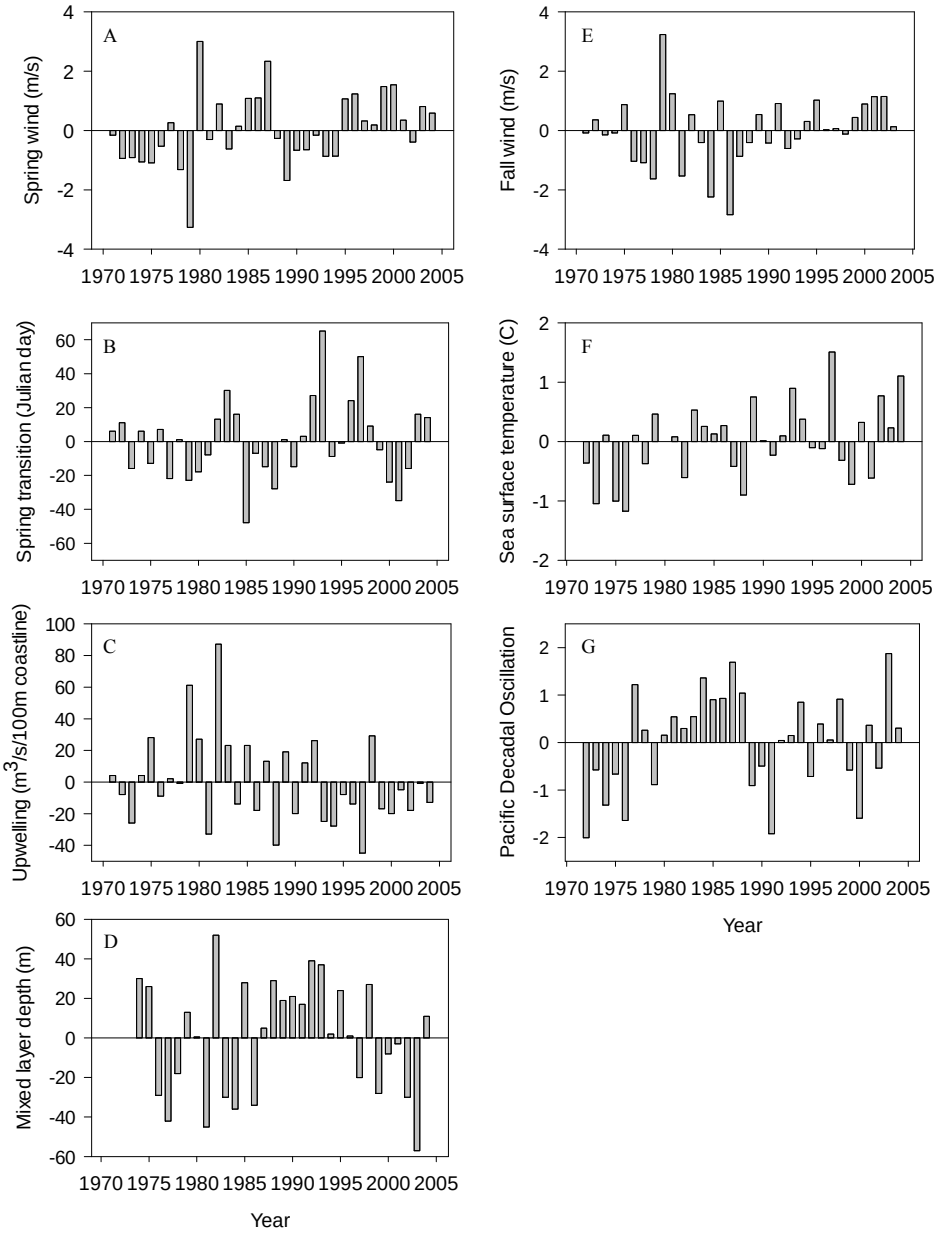

Figure 2.4 Climate indices used in our study including anomalies of spring wind speed (A), spring transition index (B), upwelling (C), mixed layer depth (D), fall wind speed (E), sea surface temperature (F), and the Pacific Decadal Oscillation index (G).

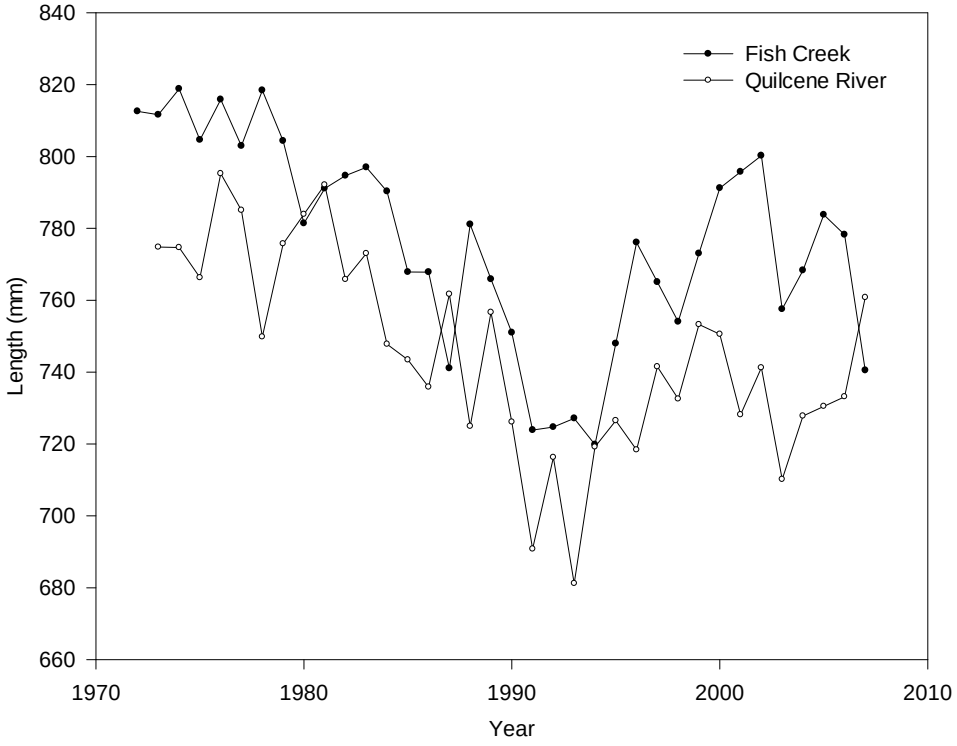

Figure 2.5 Average body length of age-0.3 male Chum Salmon (*Oncorhynchus keta*) carcasses at Fish Creek, Alaska from 1972 to 2007 and at Quilcene River, Washington from 1973 to 2007.

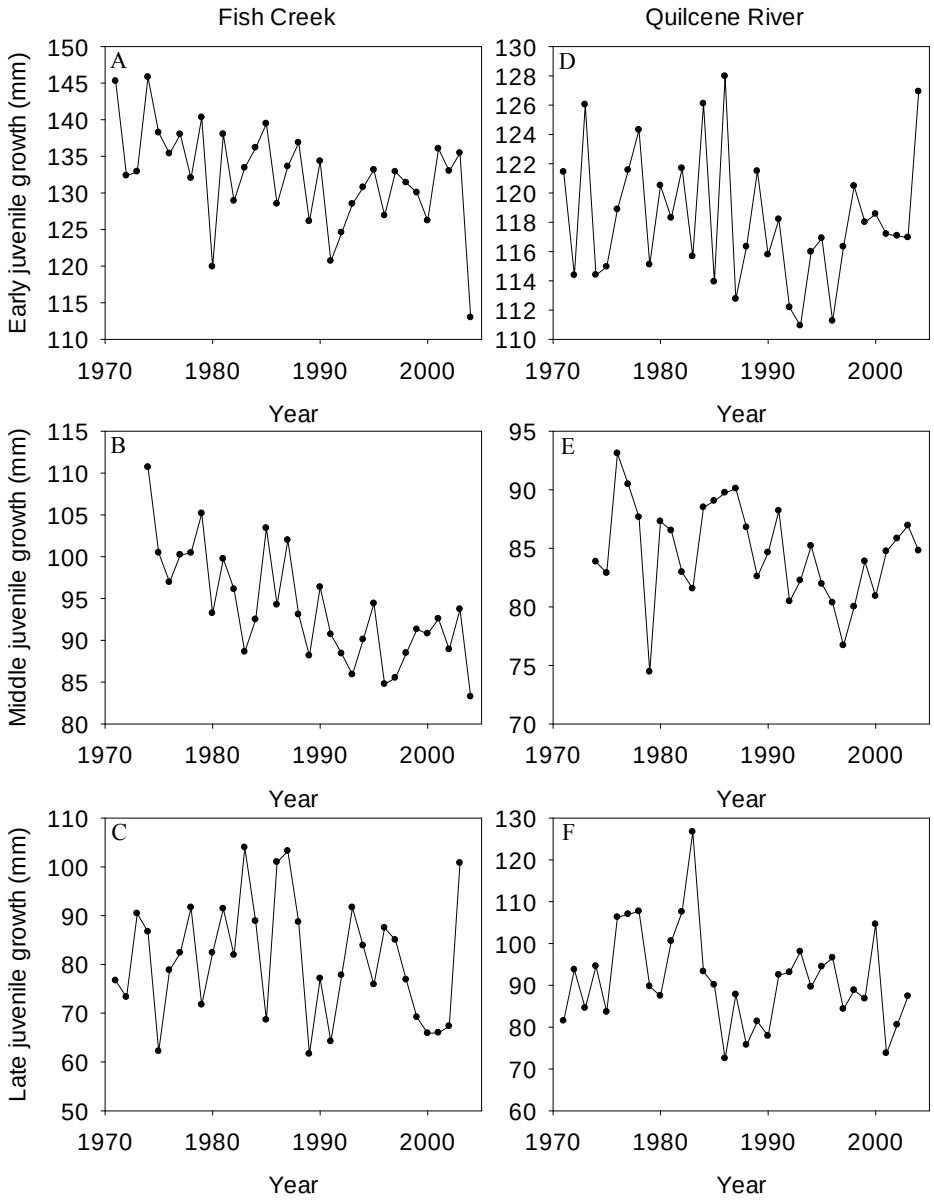

Figure 2.6 Average growth (mm) for the early (A), middle (B), and late (C) juvenile stages of age-0.3 Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska and the early (D), middle (E), and late (F) juvenile stages of age-0.3 male chum salmon from Quilcene River, Washington.

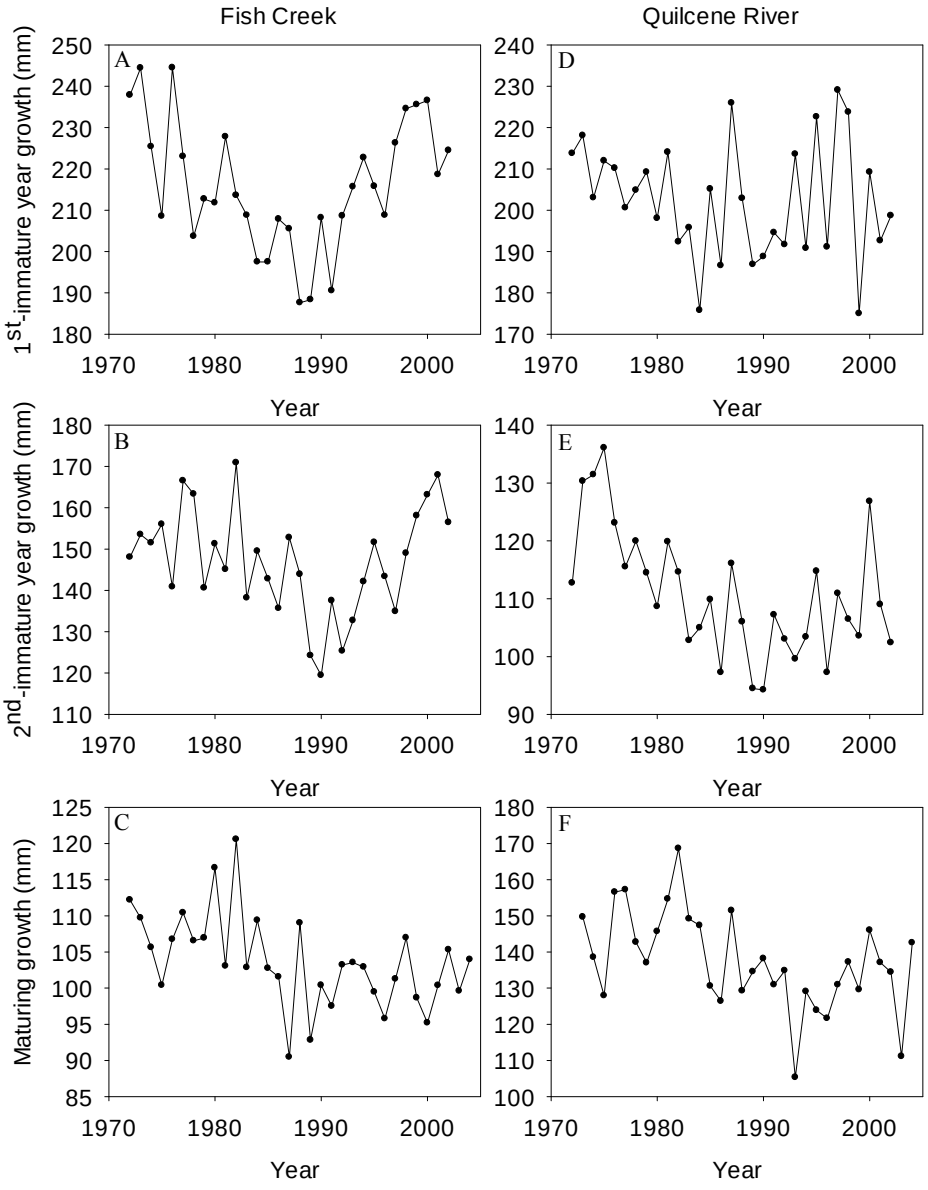

Figure 2.7 Average growth for the 1st-immature (A), 2nd-immature (B), and maturing (C) stages of age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska and the 1st-immature (D), 2nd-immature (E), and maturing (F) stages of age-0.3 male Chum Salmon from the Quilcene River, Washington.

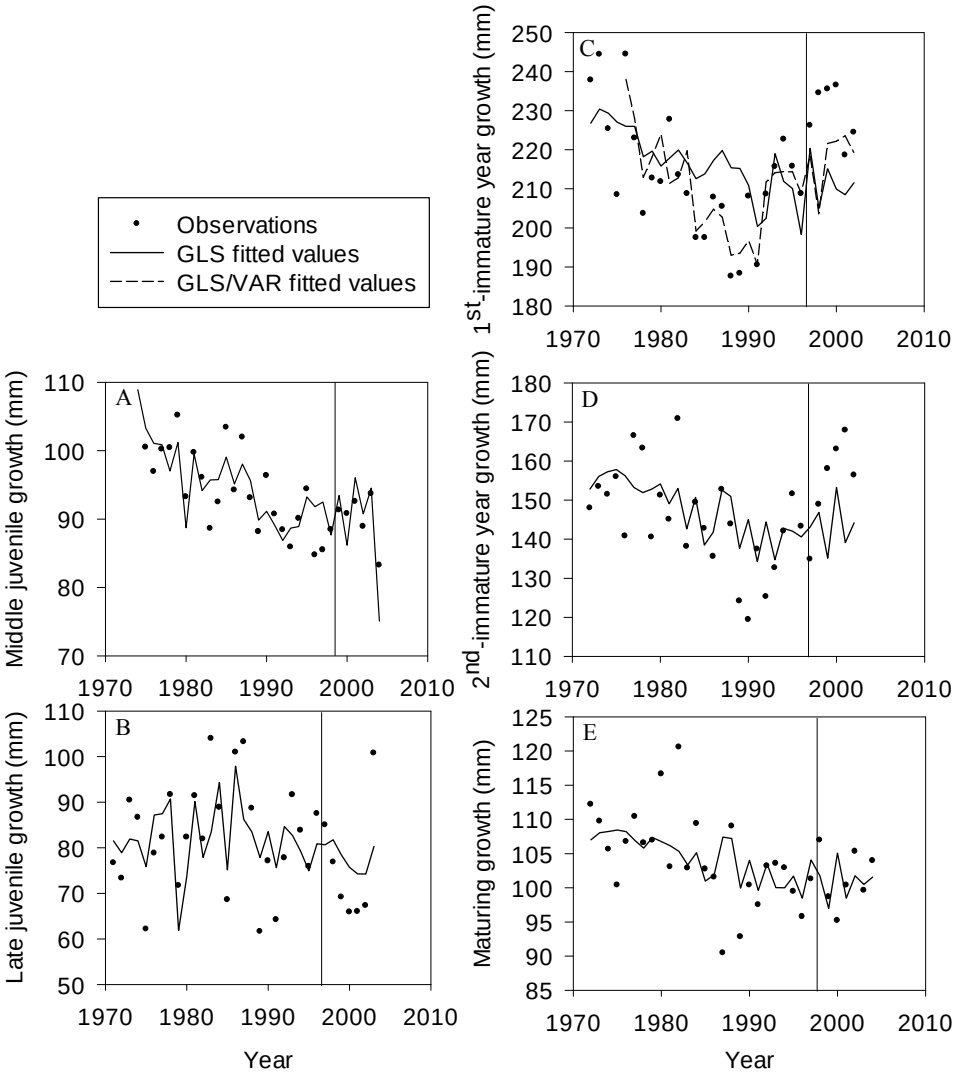

Figure 2.8 Observations and fitted values of the *in-sample* and *reserved observations* (to the right of the vertical line) for the growth of age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska using the generalized least squares (GLS) and the integrated GLS and vector autoregression error correction model (GLS/VAR).

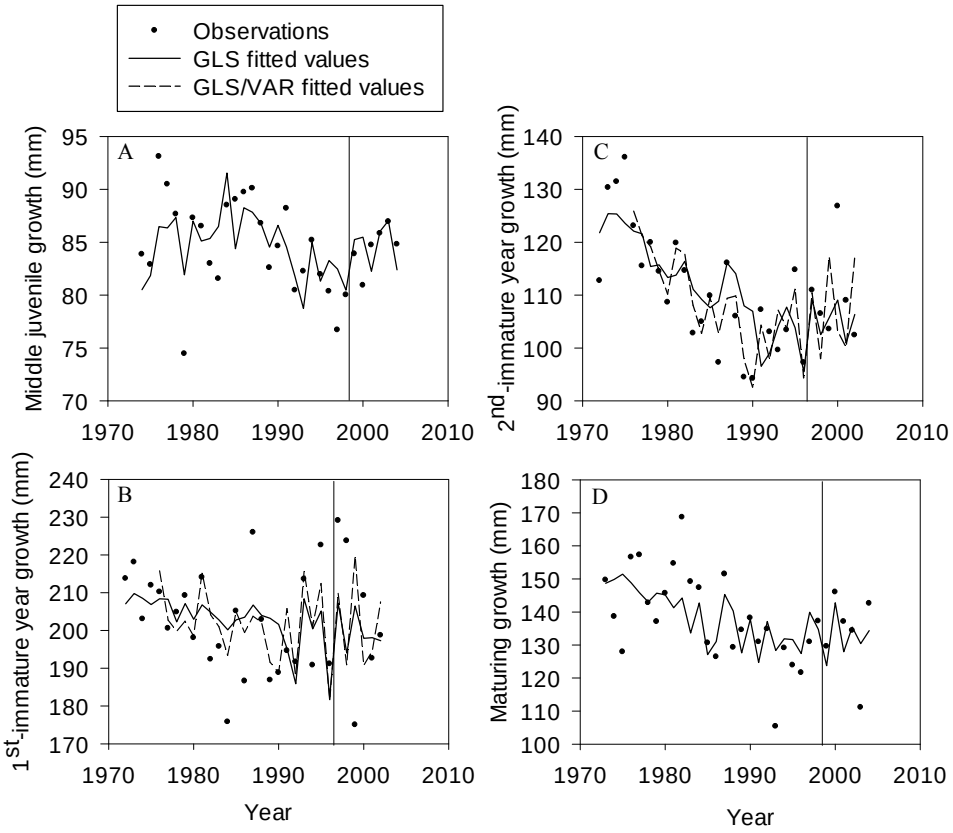

Figure 2.9 Observations and fitted values of the *in-sample* and *reserved observations* (to the right of the vertical lines) for the growth of age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Quilcene River, Washington using the generalized least squares (GLS) regression and the integrated GLS and vector autoregression error correction model (GLS/VAR).

Table 2.1 Hypothesized mechanisms and effects of selected climate indices on the marine growth of Chum Salmon (*Oncorhynchus keta*) in the North Pacific Ocean. Locations are the Gulf of Alaska (GOA), central (CNP) and eastern (ENP) North Pacific Ocean, and Washington (WA). Acronyms include the mixed layer depth (MLD), Pacific Decadal Oscillation (PDO) and sea surface temperature (SST).

Stage	Location	Index	Mechanism	Effect
Fish Creek, southern southeast Alaska (saltwater entry from Feb through May)				
Early juvenile	GOA shelf	Spring wind	Plankton bloom	-
Mid-juvenile	GOA shelf	Winter MLD	Nutrients availability	+
Late juvenile	GOA shelf	Fall wind	Fall bloom	-
Immature/Maturing	CNP ENP	Winter PDO	Cool, high nutrients	+
Immature/Maturing	CNP ENP	Summer SST	Warm	+
Quilcene River, Washington (saltwater entry in May)				
Early juvenile	WA coast	Upwelling index	Nutrient upwelling	+
Early juvenile	WA coast	Spring transition	Later upwelling	-
Mid-juvenile	GOA shelf	Winter MLD	Nutrients availability	+
Late juvenile	GOA shelf	Fall wind	Plankton bloom	-
Immature/Maturing	CNP ENP	Winter PDO	Cool, high nutrients	+
Immature/Maturing	CNP ENP	Summer SST	Warm	+

Table 2.2 Regression model variables for Chum Salmon (*Oncorhynchus keta*) from Fish Creek and Quilcene River. Models described growth as a function of length at the start of the growing season and indices of juvenile (J), immature (I), and maturing (M) Salmon abundance from southern southeast Alaska (SSEAK), southeast Alaska (SEAK), Oregon to southeast Alaska (OR-SEAK), southeast Alaska to the Alaska Peninsula (SEAK-AKPEN), Oregon and Washington (OR-WA), Oregon to British Columbia (OR-BC), Oregon to southeast Alaska (OR-SEAK), and Oregon to Alaska Peninsula (OR-AKPEN). The length variables are length at the start of the middle juvenile (La), late juvenile (Lb), 1st-immature year (Lc), 2nd-immature year (L2), and maturing year (L3) growing seasons. The abundance variable was assessed for Pink Salmon (*Oncorhynchus gorbuscha*), Chum Salmon, and the two species combined. Maturing Pink Salmon were included in the immature and maturing indices.

Dependent variable	Possible independent variables	
Growth	Length	Abundance
Fish Creek		
Early juvenile growth (*GaN*)		J_{SSEAK}
Middle juvenile growth (*GbN*)	*LaN*	J_{SEAK}, $J_{OR\text{-}SEAK}$
Late juvenile growth (*GcN*)	*LbN*	J_{SEAK}, $J_{OR\text{-}SEAK}$, $J_{SEAK\text{-}AKPEN}$, $J_{OR\text{-}AKPEN}$
1st-immature year growth (*G2N*)	*LcN*	I_{SEAK}, $I_{SEAK\text{-}AKPEN}$, $I_{OR\text{-}AKPEN}$
2nd-immature year growth (*G3N*)	*L2N*	I_{SEAK}, $I_{SEAK\text{-}AKPEN}$, $I_{OR\text{-}AKPEN}$
Maturing year growth (*G4N*)	*L3N*	M_{SEAK}, $M_{SEAK\text{-}AKPEN}$, $M_{OR\text{-}AKPEN}$
Quilcene River		
Early juvenile growth (*GaS*)		$J_{OR\text{-}WA}$
Middle juvenile growth (*GbS*)	*LaS*	$J_{OR\text{-}WA}$, $J_{OR\text{-}BC}$, $J_{OR\text{-}SEAK}$
Late juvenile growth (*GcS*)	*LbS*	$J_{OR\text{-}WA}$, $J_{OR\text{-}BC}$, $J_{OR\text{-}SEAK}$, $J_{OR\text{-}AKPEN}$
1st-immature year growth (*G2S*)	*LcS*	$I_{OR\text{-}WA}$, $I_{OR\text{-}BC}$, $I_{OR\text{-}SEAK}$, $I_{OR\text{-}AKPEN}$
2nd-immature year growth (*G3S*)	*L2S*	$I_{OR\text{-}WA}$, $I_{OR\text{-}BC}$, $I_{OR\text{-}SEAK}$, $I_{OR\text{-}AKPEN}$
Maturing year growth (*G4S*)	*L3S*	$M_{OR\text{-}WA}$, $M_{OR\text{-}BC}$, $M_{OR\text{-}SEAK}$, $M_{OR\text{-}AKPEN}$

Table 2.3 Mean, standard deviation (SD), minimum (Min.), and maximum (Max.) values of the annual means of growth (mm) back-calculated for age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska and Quilcene River, Washington.

Variable/	Fish Creek				Quilcene River			
Life stage	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Growth (mm)								
Early juvenile	132	7	113	146	118	4	111	128
Mid-juvenile	94	7	83	111	85	4	74	93
Late juvenile	81	12	62	104	92	12	72	127
1st-immature	216	16	187	224	202	14	175	229
2nd-immature	147	13	119	171	111	11	94	136
Maturing	104	6	90	121	137	13	105	169
Length at the start of the growing season (mm)								
Mid-juvenile	132	7	113	146	118	4	111	128
Late juvenile	228	11	211	257	203	7	190	218
1st-immature	309	17	276	314	295	13	175	229
2nd-immature	526	19	484	560	498	17	464	529
Maturing	673	27	620	713	609	20	568	639
Total length	777	29	720	819	746	28	681	795

Table 2.4 Mean, standard deviation (SD), minimum (Min.), and maximum (Max.) values of the abundance (in millions of fish) and climate indices used in the models.

Variable	Mean	SD	Min.	Max.
Fish Creek models	Abundance (millions of fish)			
$J_{SEAK\text{-}AKPEN,pink}$	521	230	81	1010
$I_{OR\text{-}AKPENage\text{-}0.1}$	159	72	30	313
$I_{OR\text{-}SEAKage\text{-}0.2\text{-}0.3}$	337	175	71	645
M_{SEAK}	118	74	14	166
Quilcene River models	Abundance (millions of fish)			
$J_{OR\text{-}SEAK}$	105	55	18	210
$I_{OR\text{-}AKPENage\text{-}0.1,chum}$	73	55	10	247
$I_{OR\text{-}AKPENage\text{-}0.1\text{-}0.3}$	233	103	51	426
$M_{OR\text{-}SEAK}$	90	41	19	159
Climate indices				
Fall wind velocity (m/s)	15.4	1.2	12.6	18.7
Mixed layer depth (m)	162	29	105	214
SST (°C)	11.8	0.6	10.6	13.3
PDO	0.04	1.00	-1.90	1.80

Table 2.5 *In-sample* generalized least squares (GLS) models and the integrated GLS and vector autoregression error correction models for the growth of age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska. R^2 is the coefficient of determination. WF is the fall wind speed. SST is sea surface temperature. PDO is the Pacific decadal oscillation index. J is juvenile abundance. I is immature abundance. M is maturing abundance. SEAK-AKPEN is refers to southeast Alaska to Alaska Peninsula. OR-SEAK refers to Oregon to southeast Alaska. OR-AKPEN refers to Oregon to Alaska Peninsula. Pink is the abundance of pink salmon.

Variables			Model statistics		
Growth	Explanatory	Coefficient	*P*-value	R^2	*P*-value
Middle juvenile	$Length_t$	0.632	<0.001	0.700	<0.001
	$J_{SEAK\text{-}AKPENt,pink}$	-0.522	<0.001		
Late juvenile	WF_t	-0.566	<0.001	0.386	<0.001
1st-immature	$I_{OR\text{-}AKPENt,age\text{-}0.1}$	-0.521	0.002	0.259	0.008
1st-immature	$I_{OR\text{-}AKPENt,age\text{-}0.1}$	-0.562	0.002	0.720	0.001
	$Growth_{t-2}$	0.405	0.002		
	SST_{t-2}	0.246	0.038		
	PDO_{t-1}	-0.533	<0.001		
	PDO_{t-4}	-0.216	0.017		
2nd-immature	$I_{OR\text{-}SEAKt,age\text{-}0.2\text{-}0.3}$	-0.576	0.002	0.320	0.003
Maturing	M_{SEAKt}	-0.533	0.010	0.254	0.007

Table 2.6 *In-sample* validation statistics of the growth models for age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska. GLS is the generalized least squares regression model. GLS/VAR is the GLS and vector autoregression integrated model. Statistics include degrees of freedom (df), mean, coefficient of variation (*CV*), coefficient of determination (R^2), *F*-statistic, *P*-value of the *F*-statistic, and the Schwarz's information criterion (*SIC*). Mat. is the growth of maturing salmon.

Stage/ Model	Middle Juvenile GLS	Late Juvenile GLS	1st-immature GLS	1st-immature GLS/VAR	2nd-immature GLS	Mat. GLS
df	24	25	24	16	24	25
Mean	95	82	213	210	145	104
CV	0.039	0.113	0.062	0.038	0.071	0.057
R^2	0.700	0.386	0.259	0.720	0.320	0.254
F	56.0	15.70	8.40	8.22	11.29	8.50
P	<0.001	<0.001	0.008	0.001	0.003	0.007
SIC	151	205	205	164	203	183
No. iterations				26		

Table 2.7 *In-sample* generalized least squares (GLS) models and the integrated GLS and vector autoregression error correction model for the growth of age-0.3 male Chum Salmon (*Oncorhynchus keta*) from the Quilcene River, Washington. R^2 is the coefficient of determination. MLD is mixed layer depth. SST is sea surface temperature. PDO is the Pacific decadal oscillation index. J is juvenile abundance. I is immature abundance. M is maturing abundance. OR-SEAK represents Oregon to southeast Alaska. OR-AKPEN represents Oregon to Alaska Peninsula.

Variables		Model statistics			
Growth	Explanatory	Coefficient	*P*-value	R^2	*P*-value
Middle juvenile	MLD	-0.500	0.009	0.435	0.001
	$J_{OR\text{-}SEAKt}$	0.560	0.002		
1st-immature	$I_{OR\text{-}AKPENt,chum,age\text{-}0.1}$	-0.458	0.006	0.276	0.006
	$I_{OR\text{-}AKPENt,chum,age\text{-}0.1}$	-0.471	0.004	0.466	0.020
	SST_{t-2}	0.386	0.034		
	PDO_{t-2}	-0.338	0.033		
2nd-immature	$I_{OR\text{-}AKPENt,age\text{-}0.1\text{-}0.3}$	-0.755	<0.001	0.572	<0.001
	$I_{OR\text{-}AKPENt,age\text{-}0.1\text{-}0.3}$	-0.777	<0.001	0.802	<0.001
	$Growth_{t-4}$	0.352			
	SST_{t-2}	0.309			
	PDO_{t-2}	-0.442			
Maturing	$M_{OR\text{-}SEAKt}$	-0.608	0.001	0.355	0.001

Table 2.8 *In-sample* validation statistics of the growth models for age-0.3 Chum Salmon (*Oncorhynchus keta*) from Quilcene River, Washington. GLS is the generalized least squares regression model. GLS/VAR is the GLS and vector autoregression integrated model. Statistics include degrees of freedom (df), mean, coefficient of variation (*CV*), coefficient of determination (R^2), *F*-statistic, *P*-value of the *F*-statistic, and the Schwarz's information criterion (*SIC*).

Stage	Middle Juvenile	1st-immature		2nd-immature		Maturing
Model	GLS	GLS	GLS/VAR	GLS	GLS/VAR	GLS
df	23	24	17	24	17	25
Mean	85	202	200	111	108	138
CV	0.041	0.053	0.050	0.069	0.039	0.079
R2	0.446	0.294	0.466	0.572	0.801	0.355
F	9.3	9.14	3.70	32.03	17.09	13.77
P	0.001	0.006	0.02	<0.001	<0.001	0.001
SIC	150	204	172	186	135	215
No. iterations			120		68	

Table 2.9 Validation statistics based on application of the growth models for age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek, Alaska to the *reserved observations*. GLS is the generalized least squares regression model. GLS/VAR is the GLS and vector autoregression integrated model. Statistics include sample size (*n*), mean, coefficient of variation (*CV*), coefficient of determination (R^2), *F*-statistic, *P*-value of the *F*-statistic, *F*-statistic of model deterioration (*F*-det.), *P*-value of *F*-det., and Schwarz's information criterion (*SIC*).

Stage	Middle Juvenile	Late Juvenile	1st-immature		2nd-immature	Maturing
Model	GLS	GLS	GLS	GLS/VAR	GLS	GLS
n	6	7	6	6	6	7
Mean	90	76	229	229	115	101
CV	0.047	0.140	0.090	0.068	0.108	0.046
R^2	0.460	0.423	-0.186	0.440	-0.321	0.060
F	5.10	5.14		0.94		0.450
P	0.002	0.001		0.492		0.861
F-det.	1.33	1.31		3.81		0.61
P	0.280	0.290		0.014		0.74
SIC	32	50	50	54	48	86

Table 2.10 Validation statistics based on the application of the growth models for age-0.3 male Chum (*Oncorhynchus keta*) Salmon from Quilcene River, Washington to the *reserved observations*. GLS is the generalized least squares regression model. GLS/VAR is the GLS and vector autoregression integrated model. Statistics include sample size (*n*), mean, coefficient of variation (*CV*), coefficient of determination (R^2), *F*-statistic, *P*-value of the *F*-statistic, *F*-statistic of model deterioration (*F*-det.), *P*-value of *F*-det., and the Schwarz's information criterion (*SIC*).

Stage	Middle Juvenile	1st-immature		2nd-immature		Maturing
Model	GLS	GLS	GLS/VAR	GLS	GLS/VAR	GLS
n	6	6	6	6	6	6
Mean	85	205	205	110	110	132
CV	0.029	0.100	0.124	0.076	0.124	0.073
R^2	-0.670	-0.204	-0.781	-0.034	-1.649	0.380
F						3.685
P						0.009
F-det.						0.790
P						0.586
SIC	27	51	59	40	51	41

Table 2.11 Lehmann's correlation coefficients to test the difference among the mean squared errors of the growth models for age-0.3 male Chum Salmon (*Oncorhynchus keta*) from Fish Creek and the Quilcene River. GLS is the generalized least squares regression model. GLS/VAR is the GLS and vector autoregression integrated model. Bold text indicates a 5% level of significance.

Stock		Fish Creek	Quilcene River	
Stage		1st-immature	1st-immature	2nd-immature
Sample	Method	GLS	GLS	GLS
In-sample	GLS/VAR	**0.607**	0.341	**0.636**
Out-sample	GLS/VAR	0.451	-0.640	-0.759

Chapter 3 Chum salmon (*Oncorhynchus keta*) growth and temperature indices as indicators for the year class strength of age-1 walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea[4]

ABSTRACT

Ecosystem-based fisheries management requires the development of physical and biological time series that index ocean productivity for stock assessment and recruitment forecasts for commercially important species. Since recruitment in marine fish is related to ocean conditions, we developed proxies for ocean conditions based on sea surface temperatures (SST) and biometric measurements of chum salmon (*Oncorhynchus keta*) captured in the walleye pollock (*Theragra chalcogramma*) fishery and on SST. Marine growth rates of Pacific salmon (*Oncorhynchus* spp.) are the results of a complex interplay of physical, biological, and population-based factors that fish experience as they range through oceanic habitats. These growth rates can therefore be viewed as indicators of past ocean productivity. Thus, our hypothesis is that estimated intra-annual growth in body weight of immature and maturing age-0.3 male chum salmon may be used as a biological indicator of variations in rearing conditions also experienced by age-0 walleye pollock; consequently, they may be used to predict the recruitment to age-1 in walleye pollock.

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[4] Yasumiishi, E. M., K. R. Criddle, N. Hillgruber, F. J. Mueter, and J. H. Helle. 2013. Chum salmon (*Oncorhynchus keta*) growth and temperature indices as indicators for the year class strength of age-1 pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Prepared for Fisheries Oceanography.

Growth was estimated for chum salmon sampled August 31–September 15 (1988–2009) from the bycatch of chum salmon from the commercial walleye pollock fisheries in the eastern Bering Sea. During the age-0 phase for walleye pollock, growth of chum salmon in the year of capture and the maximum of the monthly SST explained 85% of the variation in age-1 walleye pollock recruitment. Higher walleye pollock recruitment success was associated with the combined effect of a cool late summer and intermediate growth of chum salmon.

INTRODUCTION

The Bering Sea and Aleutian Island region commercial fishery for walleye pollock (*Theragra chalcogramma*), hereafter referred to as pollock, generates up to $ 454 million per year in ex-vessel revenue (Hiatt *et al*., 2011). Annual harvests of 0.8 to 1.5 million metric tons (t) are taken primarily with pelagic trawl gear. Pollock comprise over half (60%-77%) of the groundfish catches in the Bering Sea and Aleutian Islands region (Hiatt *et al*., 2011). Variations in pollock catches are largely driven by variations in the strength of incoming year-classes and annual management actions that set total allowable catch (TAC). Because there is considerable variability in survival from age-0 to age-1 (Ianelli *et al*., 2011a), there is interest in developing proxy indicators for pollock year-class strength at this early stage.

For management purposes, year-class strength for pollock is typically determined at age-1. In the eastern Bering Sea (EBS) and Aleutian Island region, age-3 and older adult pollock spawn during late winter and spring (Bacheler *et al*., 2010). Egg and larval densities are highest near Bogoslof Island (February-April), north of Unimak Pass and along the Alaska Peninsula (March-April), and around the Pribilof Islands (April-August) (Bacheler *et al*., 2010). The main pulses of spawning occur from 20 February to 31 March and from 20 April to 20 May (Bacheler *et al*., 2010). Age-0 and age-1 pollock remain on the EBS shelf, while age-2 pollock move off the shelf, and return to the EBS to spawn at age-3. Full recruitment to the commercial fishery in the Bering Sea Aleutian Island region occurs at age-6 (Ianelli *et al*., 2011a). Developing indicators for year-class

strength during the age-0 and age-1 phases will help reduce uncertainty in population estimates and expectations prior to recruitment to the fishery.

To better anticipate changes in future stock abundances it is important to understand the factors that influence survival of early life stages of pollock. Specifically, climate and ocean conditions experienced by age-0 and age-1 stages can influence recruitment success of pollock on the continental shelf of the EBS (Hunt *et al*., 2002; Quinn and Niebauer, 1995). In recent years, cooler late summer sea temperatures during the age-0 life stage were associated with higher energy prey (amphipods, euphausiids, and copepods), higher whole body energy content of age-0 pollock, and higher overwintering survival to age-1 while warmer summer sea temperatures were associated with lower energy prey, lower whole body energy content, and lower overwintering survival (Andrews *et al*., 2009; Coyle *et al*., 2011; Farley, 2009; Heintz *et al*., 2013; Moss *et al*., 2009). Hunt *et al*. (2011) hypothesized that the lower sea temperatures during summer may increase the energy stores of age-0 pollock and thereby decrease their vulnerability to predation by adult pollock and Pacific salmon (*Oncorhynchus* spp.). This was supported by the observation that these greater amounts of lipid reserves attained by the end of the first summer growing season resulted in higher overwintering survival (Heintz *et al*., 2013; Kooka *et al*., 2007; Siddon *et al*., 2013). Therefore, cooler late summer temperatures are expected to increase the recruitment of pollock to age-1.

Overwinter survival of pollock is not only affected by late summer temperatures, but also by rearing conditions experienced in winter. Age-0 pollock lose about 40% of their lipid and protein reserves during winter (Heintz and Vollenweider, 2010) and loss of

energy reserves was notably affected by rearing temperatures, with juvenile pollock in the lab using 37% less energy when reared at a cooler temperature (0.5°C) than when reared at a higher temperature (2.0°C) (Kooka *et al*., 2007). In addition, pollock with a higher body condition factors experienced lower mortality, while those with a lower body condition factors experienced higher mortality rates (Kooka *et al*., 2007). Thus, cooler winter temperatures are expected to increase overwinter survival and therefore recruitment of pollock to age-1.

In the following spring, warmer conditions and early ice retreat results in more food for pelagic species, such as age-1 pollock (Hunt *et al*., 2002; Jin *et al*., 2007; Mueter *et al*., 2006; Napp *et al*., 2000). During warm springs (1996 and 1998), the ice melts and retreats north prior to mid-March, and there is insufficient light to support an algal bloom, so the spring bloom occurs in open waters later in May or June in relatively warm water (>3°C) (Baier and Napp, 2003; Stabeno *et al*., 2001). When the bloom occurs in warm water (>3°C), copepods growth and production is higher, which in turn leads to higher growth and survival of zooplankton, larval fish, and juvenile and adult fish—a pelagic based ecosystem. Sea temperature may therefore be used to index ocean conditions that influence fish physiology and survival; however, a biological indicator that integrates these habitat conditions may present a more reliable predictor for pollock recruitment success.

Salmon growth may be a better measure of growth conditions during a given year than, for example, any one of the hydrographic factors mentioned above because it integrates actual ocean productivity through the entire growth period. For example,

marine growth of chum salmon (*O. keta*) was significantly correlated with air temperature (Helle, 1979), sea temperature (Agler *et al*., 2013; Kaeriyama *et al*., 2007), dew point (Helle, 1979), cloud cover (Helle, 1979), sea ice concentration (Agler *et al*., 2013; Kaeriyama *et al*., 2007), and zooplankton biomass (Seo *et al*., 2006). Therefore, growth of chum salmon derived from salmon scale patterns may be a reasonable proxy for this suite of environmental correlates because it reflects ecosystem productivity through time and across space used by chum salmon.

In this study, we hypothesize that growth of chum salmon can be used as an indicator of ocean conditions that equally affect pollock survival. In the Bering Sea/Aleutian Island trawl fishery, chum salmon were captured primarily in the southern continental shelf region in the EBS during the B Season (June 10th to late October) in 2004 (Stram and Ianelli, 2009). Age-0 pollock distribute primarily in the middle (50-100 m isobaths) and outer (100-200 m isobaths) domains while chum salmon are caught in the outer domain of the EBS (Parker-Stetter *et al*., 2013; Stram and Ianelli, 2009). Adult chum salmon are both, a predator and competitor of age-0 and age-1 pollock (Coyle *et al*., 2011). The spatial and temporal co-occurrence of chum salmon and pollock provided an excellent opportunity to use the growth of bycaught chum salmon as an index of the integrated effect of ocean productivity as it pertains to the recruitment of age-1 pollock. For age-0 pollock, the index of total lipid content was more closely correlated with mean body weight than with mean length (Heintz *et al*., 2013). Therefore, in order to better reflect lipid content, growth was indexed in terms of salmon body weight rather than length.

The overall goal of this project was to develop low cost indicators for pollock recruitment. The specific objectives were to: (1) develop an index of growth in body weight from scale patterns of chum salmon as an indicator for ocean productivity for pollock during the age-0 life stage, (2) develop a composite index for optimal sea temperatures for pollock during the age-0 and age-1 life stages, and (3) evaluate the growth and temperature indices as predictors for the abundance of age-1 pollock. We hypothesize that the growth of immature and maturing chum salmon sampled at sea, summer sea temperatures, and temperature composite indices may be used as effective proxies for ocean productivity on the continental shelf of the EBS, an important rearing habitat for young groundfish and immature and maturing chum salmon. Specifically, increased salmon growth, a cool late summer, cool winter, and warm spring sea surface temperatures (SST) will increase the survival of pollock to age-1 and subsequent year-class strength.

METHODS

The basic model sets out to describe the estimated year-class strength of age-1 pollock as a function of salmon growth during the age-0 stage and of temperature conditions during the age-0 and age-1 stage.

Pollock recruitment index

The estimated abundance of age-1 pollock was selected as the dependent variable in our models. Numerical estimates of the abundance of age-1 pollock (millions of fish) in the EBS (Fig. 3.1) were obtained from North Pacific groundfish stock assessment and fishery

evaluation reports (Table 1.25 in Ianelli *et al*., 2011a). These estimates are based on age-structured models that use fishery and survey data to estimate pollock abundances. Abundance estimates of age-1 pollock ranged from 3,999 million in 2005 to 49,702 million in 1990 with an average of 21,764 million fish.

Summer sea temperature and temperature composite indices

Summer SST and temperature composite (TC) indices were constructed from average monthly SSTs. Data were obtained from the National Oceanic and Atmospheric Administrations' Earth System Research Laboratory's Physical Sciences Division website (http://www.esrl.noaa.gov/psd/data/timeseries/). SST was based on National Centers for Environmental Prediction/National Center for Atmospheric Research gridded reanalysis data (Kalnay *et al*., 1996). Indices were calculated for an area in the southeastern Bering Sea (56.2° and 58.1°N latitude by 166.9° and 161.2°W longitude) observed to be heavily used by chum salmon (Stram and Ianelli, 2009) and age-0 and age-1 pollock (Parker-Stetter *et al*., 2013). Summer SST was constructed as the maximum of the monthly mean SST in each year, August or September. Winter SST was constructed as the average of the monthly SST values for January through March, the coldest months of the year. Spring SSTs were constructed as the average of the monthly SST for June, to reflect the optimum timing of the spring bloom.

Three TC indices were developed. In contrast to the TC index in Martinson *et al*. (2012), these TC indices are based on time series of normalized SSTs. Positive TC index values were used to represent favorable conditions of a cold late summer (year *t-1*) during the age-0 stage, cold winter between the age-0 and age-1 stages, and a warm spring (year

t) during the age-1 stage, while negative values represent less favorable conditions of a warm late summer (year *t-1*) during the age-0 stage, warm winter between the age-0 and age-1 stage, and a cold spring (year *t*) during the age-1 stage. The TC1 index was calculated for each year as the as the sum of the positive sign of the spring SST in year *t* and negative sign of the late summer SST in year *t-1*. The TC2 index was calculated for each year as the sum of the negative sign of the winter SST in year *t* and negative sign of late summer SST in year *t-1*. The TC3 index was calculated for each year as the sum of TC2 index and positive sign of the spring SST for year *t*. To equally weight each life history stage we normalized each seasonal SST time series by subtracting the mean and dividing by the SD. Data for years 1988–2009 were used to match the years of the growth data.

Growth index

Growth in the final year at sea was estimated for male age-0.3 chum salmon captured in the commercial fishery for pollock in the EBS. A total of 399 age-0.3 male chum salmon taken incidentally in the pollock fishery during the B Season (June 10-late October) in 1988, 1990, 1998–2002, and 2004–2009 (n = 13 years) were selected for this study. To reduce temporal variability in growth only fish from September 1–15 were selected; if samples sizes were less than 30, fish from August 31 were added to supplement sample sizes. For each fish, scales were collected and sex, fork length to the nearest 1.0 mm, wet weight to the nearest 1.0 g, and maturity were recorded. Only scales from the preferred area were selected and read for age.

Using Image Pro[2] digitizing software, a reference line was drawn on the scale image from the focus to the edge of the scale along the longest anterior axis of the scale. The third annulus and the edge of the scale were identified by visual inspection. All measurements were exported to a data file that was used to calculate annual mean distances along the scale radius from the focus to the third ocean annulus and for the total scale radius. These measurements were used to estimate chum salmon growth in length at the start of the growing season at age-0.3.

Average growth in body weight of chum salmon during the final year at sea was estimated using average total body weight, average total body length, estimated average body length and weight at the start of the growing season, average total scale radius, and average scale radius from the focus to the third marine annulus. First, a linear regression model was fit to the annual average values of total body length and total scale radius. The relationship between the average body length $(L_{age-0.3^+})$ and average scale radius $(S_{age-0.3^+})$ of the age-0.3 chum salmon at the time of capture was given as:

$$\hat{L}_{t,age-0.3^+} = \hat{b} + \hat{m}(S_{t,age-0.3^+}) + \hat{e}_t \quad (1)$$

where t was year, $\hat{b}$ was the estimated intercept, $\hat{m}$ was the estimated slope, age-0.3^+ was the age at the time of capture in September (+), and e_t was a normally distributed random variable centered on 0. The estimated coefficients in Eqn 1 were used with the average scale radius from the focus to the third marine annulus $\hat{S}_{t,age-0.3}$ to obtain predicted values for $\hat{L}_{t,age-0.3}$, average length at the start of the growing season. This estimated average

[2] Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length at the start of age-0.3 on January 1 was adjusted for the deviation of the model using the relationship described as:

$$\tilde{L}_{t,age-0.3} = \left(\frac{L_{t,age-0.3^+}}{\hat{L}_{t,age-0.3^+}} \right) \hat{L}_{t,age-0.3} \quad (2)$$

where age-0.3 is the age at the start of the age and year on January 1. The circumflex accent (^) symbol represents values estimated from the coefficients obtained from the generalized least squares model while the ~ symbol denotes values obtained after adjusting for the deviation in length from Eqn 1.

A growth curve for chum salmon for the relationship between the annual average of the total body weight and total body length at capture was estimated as:

$$W_{t,age-0.3^+} = \hat{a}\left(L_{t,age-0.3^+} \right)^{\hat{b}} \hat{u}_t \quad (3)$$

where a and b are unknown constants to be estimated and u_t is a log-normal random variable centered on 1. The model was log-transformed to estimate the coefficients ($\hat{a}$ and $\hat{b}$). The estimated coefficients in Eqn 3 and values of estimated length at the start of the growing season $\tilde{L}_{t,age-0.3}$ were used to obtain predicted values for weight at the start of the growing season $\hat{W}_{age-0.3}$. Then the estimated average body weight at age-0.3 was adjusted for the deviation of observed total average body weight from the expected average body weight based on the growth curve.

$$\tilde{W}_{t,age-0.3} = \left(\frac{W_{t,age-0.3^+}}{\hat{W}_{t,age-0.3^+}} \right) \hat{W}_{t,age-0.3} \quad (4)$$

Growth in body weight of chum salmon during the final year at sea ($\tilde{G}$) was calculated as the difference between the estimated average body weight at age-0.3 and the observed average body weight at capture.

$$\tilde{G}_t = W_{t,age-0.3^+} - \tilde{W}_{t,age-0.3} \quad (5)$$

Data analysis

A generalized least squares regression model was used to describe age-1 recruitment of pollock as a function of chum salmon growth, summer SST, and the temperature composite indices:

$$R_t = \beta_1(\tilde{G}_{t-1}) + \beta_2(\tilde{G}_{t-1})^2 + \beta_3(SST_{t-1}) + \beta_4(SST_{t-1})^2 + \beta_5(TCx_{t-1}) + \varepsilon_t \quad (6)$$

where R_t is recruitment of pollock to age-1, $\tilde{G}_{t-1}$ is the estimated growth of salmon (from Eqn 5) corresponding with the age-0 pollock phase, TCx is one of the three temperature composite indices associated with the age-0 and age-1 phase and ε_t are the residuals with mean zero and a constant variance.

The time series on growth and SST were fragmented; therefore the predictor variables were lagged to the recruitment variables prior to the analysis in effort to not lose additional years of data. Although hypotheses were specified for positive relationships between recruitment and the growth and temperature indices, we included a squared term for growth and SST to account for possible nonlinear relationships. Log transformation on the predictor and response variables did not result in a linear relationship between growth and recruitment. All sets of observations were transformed

into scale-free values by subtracting their sample mean and dividing by their standard deviation (Gollub and Van Loan, 1989).

Selection of the best fit model was based on the lowest Schwarz's information criterion (*SIC*). To determine the significance of the predictor variables in the model we added each predictor separately. Parameters with a significant *t*-value under the critical *t*-value were included in the model. Simetar software program for Excel was used in the regression modeling (Simetar, Simetar Inc., College Station, TX; Excel 2007, Microsoft Corp., Redmond, WA).

Assumptions tested for linear regression modeling included heteroscedasticity of the residuals (Goldfeld-Quandt, absolute residuals vs. fitted values plot), normality (qq plots, studentized residuals vs. fitted values, and Shapiro test), multicollinearity (Pearson correlation), and tests for the equivalency of competing model specifications (e.g., *SIC*). The degrees of freedom were calculated for the generalized least squares model (n-k) with the number of observations in the data set (n) and the number of coefficients in the model (k).

RESULTS

Variables used in calculating estimated growth in body weight $\left(\tilde{G}_t\right)$ of the age-0.3 male chum salmon bycaught in the pollock fishery are listed in Table 3.1.

There was a linear relationship between total length and scale radius for a sample of age-0.3 male chum salmon bycaught in the EBS pollock fishery $(L_{age-0.3^+} = 199 \cdot S_{age-0.3^+} + 37)$ (Fig. 3.3). The model fit was statistically significant

($P = 0.009$), but had only modest explanatory power ($R^2 = 0.477$). The estimated slope coefficient was statistically significant ($P = 0.009$) while the intercept was not ($P = 0.840$). Residuals of the model passed the test for normality (S-W = 0.964, $P = 0.819$) and constant variance ($P = 0.172$). The regression model was used to estimate length at age-0.3, at the start of the growth season.

A growth curve was fit to total average body weight and total average fork length ($W_{age-0.3^+} = 1.16^{-10}\left(L_{age-0.3^+}\right)^{3.694}$, $R^2 = 0.938$, $P < 0.001$) (Fig. 3.4). Residuals passed the test for normality (S-W = 0.957; $P = 0.709$) and a constant variance ($P = 0.821$). The estimated length at age-0.3 was fed into the growth curve to estimate body weight at age-0.3. Body weight at age-0.3 was adjusted for the deviation of total body weight from the total body weight estimated from the growth curve.

Growth in body weight during the third year at sea was estimated as the difference between total body weight at capture and the estimated body weight at age-0.3. Growth had a high degree of variability and ranged from 0.85 to 1.78 kg yr^{-1} (Fig. 3.5), with particularly high anomalies in 1988 and low anomalies in 2004, 2007, and 2009.

There was a significant correlation between recruitment of age-1 pollock and SST, but growth was not correlated with either the temperature indices or the pollock index (Table 3.2). Also, because the SST and TC2 indices were highly collinear, they could not both be included in the regression model.

In the regression models (Table 3.3) and scatter plots (Fig. 3.6), individually SST, TC1, TC2, and TC3 were significant predictors of age-1 pollock recruitment. In the single predictor models, in order of significance, the variation in age-1 pollock

recruitment was best explained by SST (*SIC* = 262, R^2 = 0.679), TC3 (*SIC* = 270, R^2 = 0.388), TC1 (*SIC* = 270, R^2 = 0.321), and TC2 (*SIC* = 270, R^2 = 0.317). Growth was not statistically significance but explained 40% of the variability in recruitment (*SIC* = 273, R^2 = 0.404).

Observed, fitted, and residuals of each statistically significant model are shown in Fig. 3.7. When including multiple predictors in the model, the model with the lowest *SIC* (257) included growth and SST (Table 3.3, Model F). This model also had the best performance (Table 3.4). Growth was introduced as a nonlinear predictor of age-1 pollock and SST as a linear predictor of age-1 pollock and these two predictors explained 85% of the variability in the age-1 pollock recruitment index ($P < 0.001$). Growth explained an additional 17% of the variation in recruitment above SST alone. The second best fit model included only SST (Model B). Pollock recruitment was negatively correlated with summer SST during the age-0 phase and explained 68% of the variability in pollock recruitment to age-1 (Model B). The model with the third lowest *SIC* (266) included growth and TC3 (Model H). Together these variables explained 63% of the variability in pollock recruitment to age-1. However, the inclusion of temperature during the winter and early spring as indexed by TC1, TC2, and TC3 did not improve the model fit over including late summer SST alone. For models that included growth, age-1 recruitment was generally under estimated in odd-numbered years and overestimated in even-numbered years (Fig. 3.6). Residuals of all models were normally distributed.

DISCUSSION

One important goal in the assessment of fish populations is the attempt of decreasing the amount of uncertainty in estimates of population abundance. In order to address this problem, there is a need to index those processes that may be affecting the survival rates of fish populations. In this study, we explored the usefulness of four temperature indices as proxies for ocean conditions experienced by age-0 and age-1 pollock in the EBS and we evaluated the observed growth of co-occurring chum salmon as a proxy for pollock rearing conditions beyond simple temperature indices alone. In our models, the maximum of the monthly summer SST and the growth of age-0.3 immature and maturing ocean-caught chum salmon together were the best predictors for the recruitment of age-1 pollock one year later.

Different climate models predict increases in sea temperature in the EBS. For example, sea and air temperatures are expected to increase and remain highly variable in the EBS (Wang *et al*., 2012). Also, the Intergovernmental Panel on Climate Change model (IPCC, 2007) projects a 1°C increase in SST from 9°C to 10°C from 2010 to 2050 for the EBS region (Ianelli *et al*., 2011b). The largest increases in air temperature in the EBS are expected to occur in the fall, with increases of 3°C by 2050 (Wang *et al*., 2012). These changes in hydrographic conditions will undoubtedly have far-reaching effects throughout the Bering Sea. Namely, warming is expected to result in an earlier ice retreat and increased primary productivity. Wang *et al*. (2012) predict that the timing of the maximum southern extent of sea ice (March-May) will be reduced by 58%, with ice free conditions in December. An earlier ice retreat is also expected to results in an increase in

the magnitude of the spring bloom (Brown and Arrigo, 2013). However, warming conditions throughout the year may also reduce the spawning biomass of pollock, reduce the recruitment success of pollock, and may ultimately result in lower catch limits (Ianelli *et al*., 2011b). Our finding that the maximum monthly SST ranging from 8.7–12.1°C in the southern EBS during the age-0 phase was inversely related to age-1 pollock recruitment success in the following year supports the prediction that pollock recruitment is likely to decrease in the EBS in response to a future warming trend.

Variations in pollock recruitment in the EBS were also linked to other life stages and oceanic conditions. For example, for the period of 1988–2008, age-0 pollock were more abundant in warm years (Smart *et al*., 2012a). Also, there was a positive effect of temperature on the abundance of eggs, yolk-sac larvae, and preflexion larvae for intermediate temperatures; and positive effects on the abundances of late larvae and juveniles at high and low SSTs (Smart *et al*., 2012b). In addition, in warm years age-0 pollock were transported from the outer shelf to the middle and inner shelf and away from the adult pollock distribution, thereby reducing their exposure to cannibalism (Wespestad *et al*., 2000). During the age-0 and age-1 phases, a dome-shaped relationship between age-1 pollock survival and summer SST was observed (Mueter *et al*., 2011). In contrast, we found that the early winter and late spring SSTs during the age-1 phase of pollock were not linked to recruitment. It is apparent from these diverging results that further research into development of environmental composite indices is needed to account for nonlinear effects of rearing conditions on recruitment at various life stages.

Chum salmon growth was a nonlinear predictor of pollock recruitment. The abundance of age-1 pollock was highest at intermediate levels of chum salmon growth. A portion of this relationship may be explained by climate- or size-related changes in salmon feeding patterns. In the EBS, chum salmon consumed a higher proportion of age-0 pollock (less energy-rich prey) during warmer summers when age-0 pollock were more abundant (2003–2005), whereas chum salmon consumed a more lipid-rich diet of crustaceans during cooler summers (2006–2008) when age-0 pollock were less abundant (Coyle *et al*., 2011). Presumably, the consumption of lower levels of age-0 pollock that led to higher age-1 abundances was linked to intermediate growth of the chum salmon in our population. As chum salmon increase in size, they often switch to feeding on gelatinous zooplankton (Davis *et al*., 2009). Unfortunately, to date only very little is known about the climate-related changes in abundance and distribution of gelatinous zooplankton in the EBS. Further studies are needed to understand the mechanism driving this relationship between salmon growth and pollock abundance.

An alternating year pattern in the residuals of our models indicates a possible interaction with the release of pink salmon from Asia (Ruggerone and Nielsen, 2004). Specifically, the model with salmon growth and SST underestimated the recruitment of age-1 pollock in most odd-numbered years, corresponding to even years of salmon growth. Asian pink salmon are up to four times more abundant as adults in the Bering Sea in odd-numbered years (Azumaya and Ishida, 2000). Other studies document the effects of pink salmon abundances on the feeding of chum salmon. For example, in odd-years of higher pink salmon abundances in the ocean, chum salmon consume less prey

(Salo, 1991), shift their diet to less nutritious prey (Salo, 1991), and switch from eating crustacean to gelatinous zooplankton (Tadokoro *et al*., 1996). We would expect to underestimate pollock abundance in even-years with the odd-years growth. However, chum salmon from the Bering Sea are less abundant in the Bering Sea during odd-numbered years due to a density-dependent migration south into the central Pacific Ocean to avoid interaction with pink salmon (Azumaya and Ishida, 2000). Thus, chum salmon remaining in the Bering Sea may experience greater intra-specific competition in the Bering Sea in even-numbered years, when fewer pink salmon are present.

Several factors may affect the predictive ability of our salmon growth index for fish recruitment. The biological characteristics of chum salmon sampled from the pollock fishery may vary between years due to factors other than environmental conditions, such as changes in sampling methods, timing of sampling, and stock composition of the samples. We accounted for season, area, age, and sex, but not for stage of maturity, stock origin, or sampling method, due to the small sample size; however, the factors may have impacted the results.

Chum salmon captured in the Bering Sea represents a mixture of stocks originated in Asia and North America. And stock origin can significantly affect growth of chum salmon (Helle, 1995). In addition, the origin of salmon in the EBS pollock fishery can vary by year for a specific season, area, and age (Wilmot *et al*., 1998). During the fall of 2002, immature chum salmon collected in the EBS and Aleutian Islands originated from Japan, Russia, and the United States (Kondzela *et al*., 2005). Genetic stock identification indicated that chum salmon captured in the pollock commercial fishery in 1994 were 39-

55% Asian, 20-35% western Alaska, and 21-29% southeastern Alaska, British Columbia and Washington (Wilmot *et al*., 1998). In contrast, the origin of chum salmon taken as bycatch in 1995 was estimated to be 13-51% Asian, 33-53% western Alaskan, 9-46% southeastern Alaskan, and 9-45% from British Columbia or Washington (Wilmot *et al*., 1998). To reduce intra-annual variability in growth due to stock origin, future sample design would benefit from further stratification by stock origin, but would undoubtedly require a large amount of additional fish sampling.

Sampling design may have also influenced the growth index. NMFS observers were required to be on-board of vessels in the 60´-125´ size class for 30% of the fishing days in a quarter. And the days spent on-board were decided by the skipper. Only catcher vessels 125´ and longer were required to have 100% of observers-coverage during the fishing days. Pella and Geiger (2009) suggested that sampling design should be more uniform across season, area, fish sizes, hauls, deliveries, and vessels. Stocks can differ in size at age and still migrate together in the ocean, therefore, size selectivity and nonrandom sampling may affect the precision of chum salmon growth as indices for ocean productivity. However, precision of the growth index is only affected if the sampling bias is inconsistent over time.

Growth indices of age-0.3 chum salmon used in this study were not correlated with summer SST or with temperature composite indices. This surprising result may be due to the overriding influence of other environmental factors impacting salmon growth. For example, Seo *et al*. (2006) found that the growth rates of age-0.1, age-0.2, and age-0.3 chum salmon that returned to Korea from 1984 to 1998 were correlated with

zooplankton abundance in the EBS. In the subarctic domain of the western North Pacific, back-calculated growth of chum salmon was positively correlated with sea surface salinity, but not with SST, for 1979–1998 (Morita *et al*., 2001). In addition, a bioenergetics model of growth indicated that size at maturity of chum salmon was regulated more by prey zooplankton density than SST for 1970–2000 (Kishi *et al*., 2010). These studies emphasize the fact that fish growth is the end product of multiple, and sometimes even interacting, factors (temperature, salinity, pH, turbidity, and prey abundance, composition, and condition), so that chum salmon growth in this study, could be used as a more comprehensive proxy for rearing conditions experienced by juvenile pollock. It is possible that it is this composite quality of growth in particular that makes it such a valuable predictor for pollock recruitment to age-1 in the EBS as revealed in this study.

CONCLUSIONS

In assessing the status of pollock in the EBS, the development of quantitative indices of ocean conditions and productivity experienced by fish prior to their recruitment to the commercial fishery provides a quantitative measure to support the predictions of above or below average recruitment (Ianelli, *pers. comm*.). The finding that the combination of physical and biological indices was a better predictor of pollock recruitment than either of these indicators alone further supports the assessment of using biological indices such as salmon growth as indicators of ocean productivity and fish recruitment. Future analysis should focus on improving salmon growth as an index of pollock recruitment by

stratifying growth data to include only fish from a single origin and by extending the survey to cover a longer time period. Further assessment is also needed to evaluate these environmental composite indices in stock-recruitment models over a longer time period and further explore their value by using them in forecasting models.

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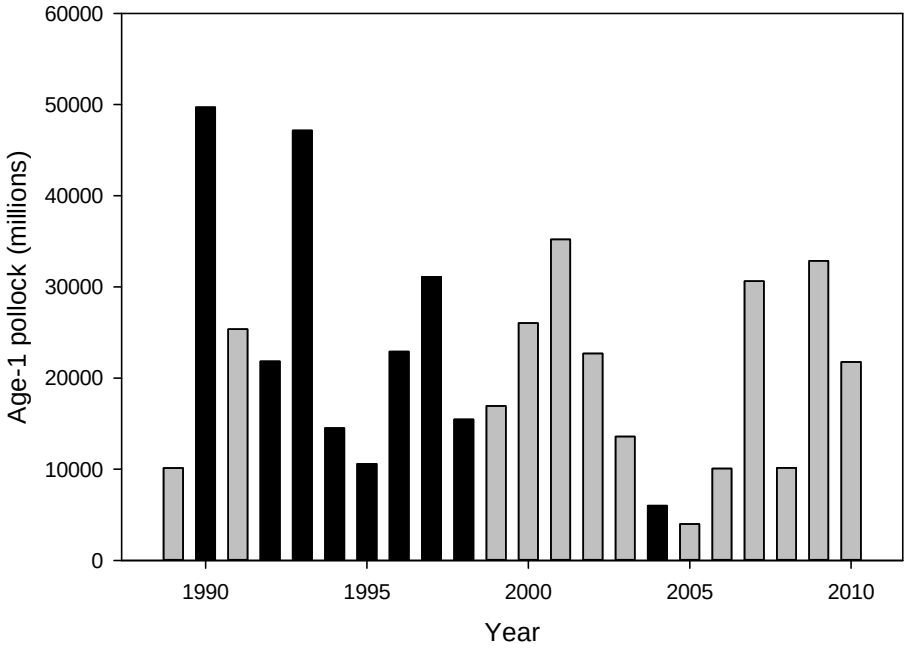

Figure 3.1. Estimated annual abundance of age-1 walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (Ianelli *et al*., 2011a). Years with gray bars were used in our analysis.

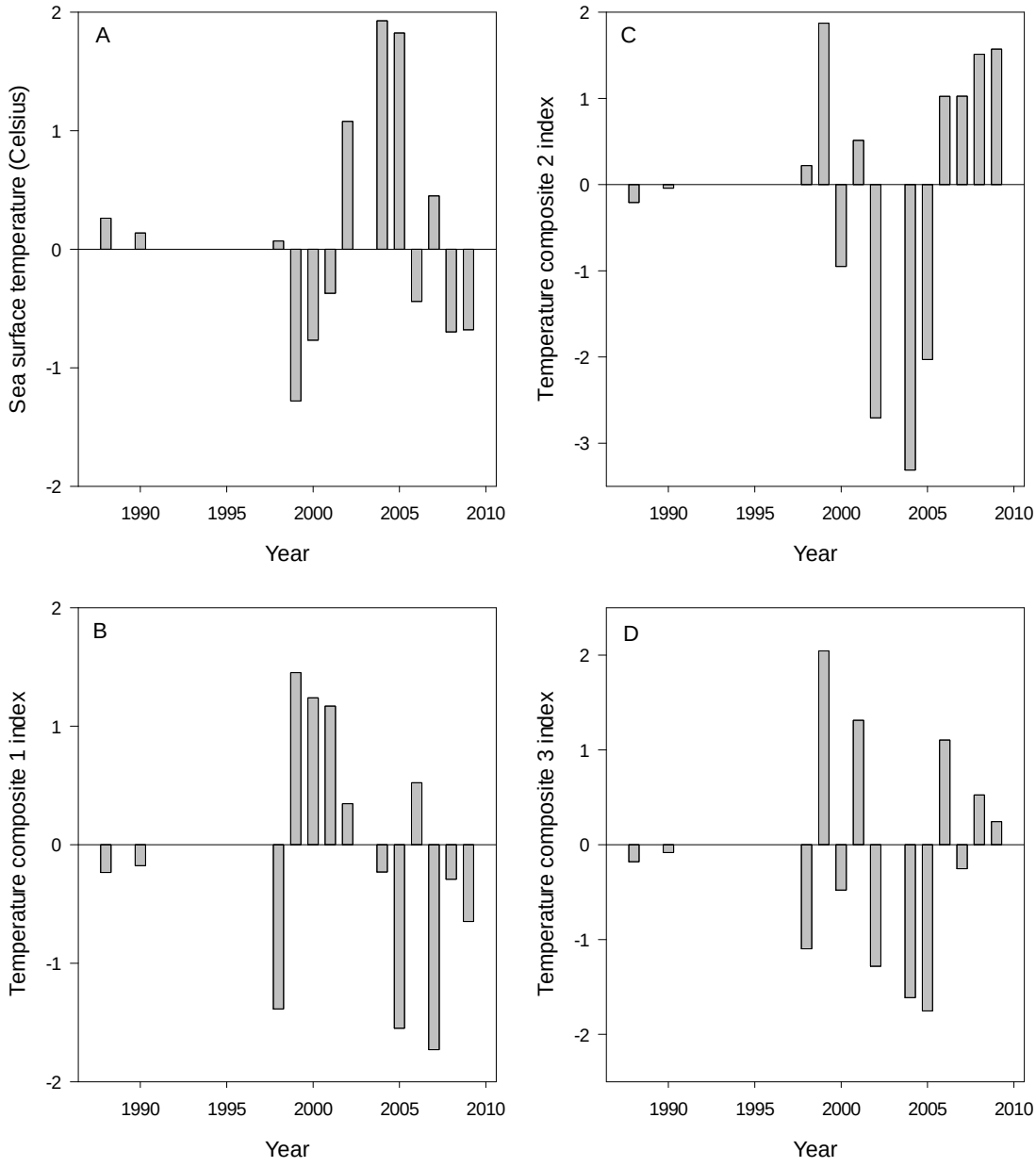

Figure 3.2. Normalized temperature indices for the southeastern Bering Sea. Temperature indices include (A) summer sea surface temperature, (B) temperature composite 1 index, (C) temperature composite 2 index, and (D) temperature composite 3 index.

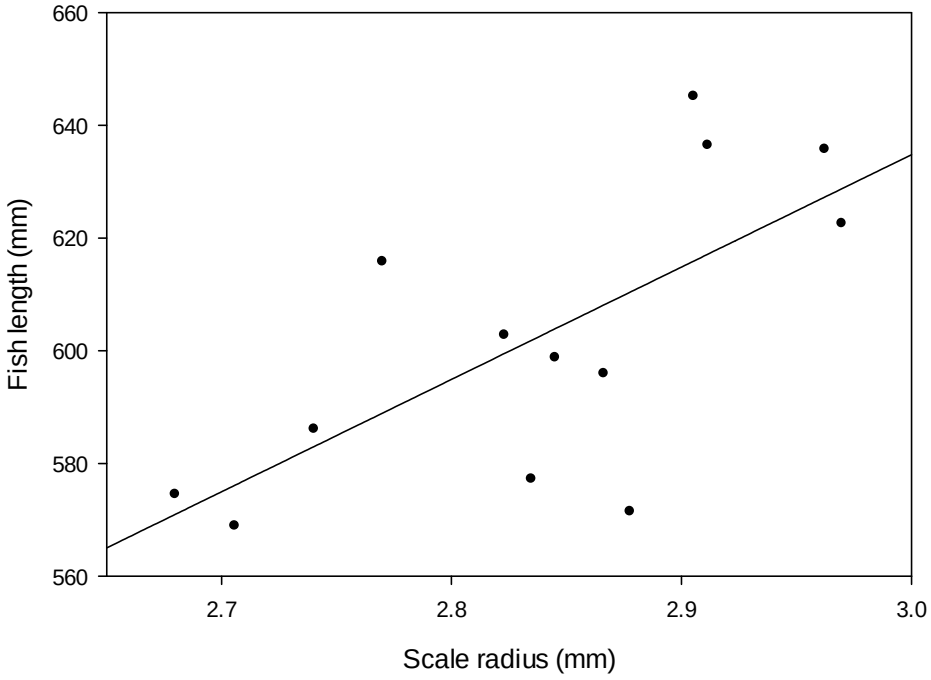

Figure 3.3. Linear regression line of fish length and scale radius for a sample of age-0.3 male chum salmon bycaught in the pollock fishery in the eastern Bering Sea.

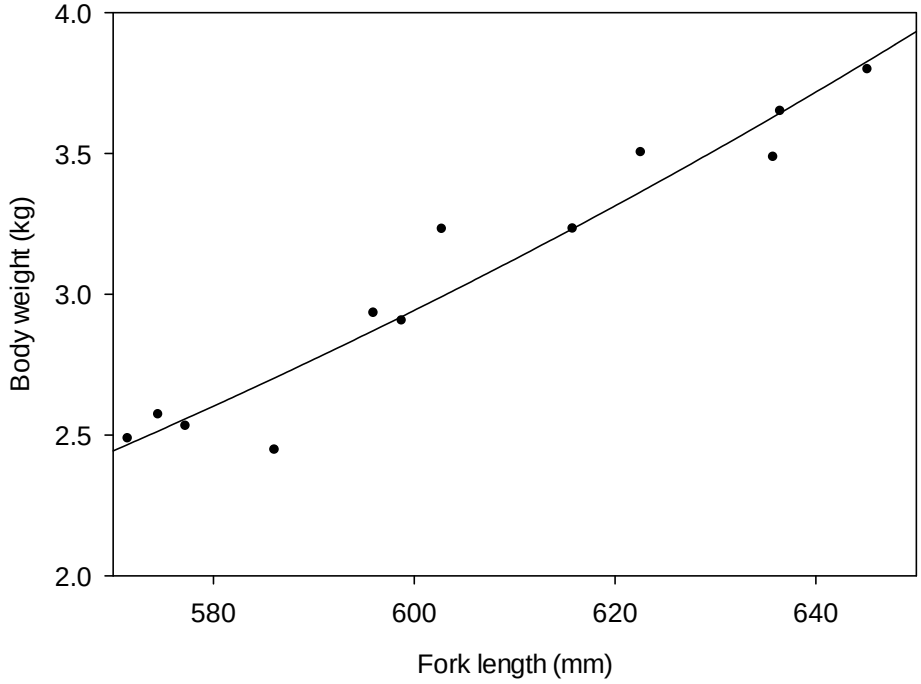

Figure 3.4. Annual mean body weight and fork length relationship for age-0.3 male chum salmon samples from the bycatch in the commercial pollock fishery in the eastern Bering Sea.

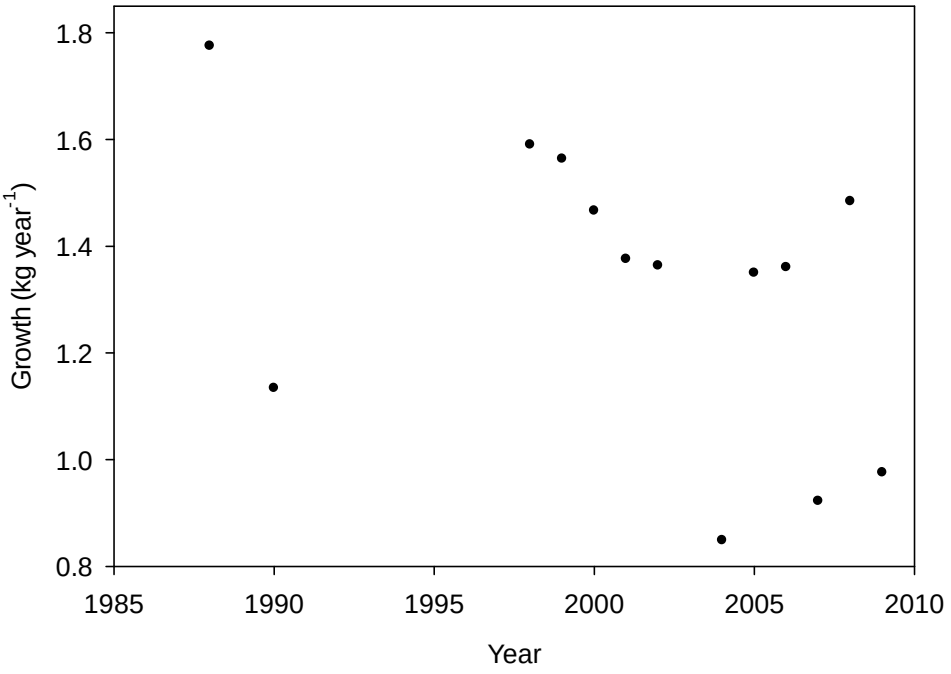

Figure 3.5. Estimated average annual growth of age-0.3 male chum salmon captured in the eastern Bering Sea pollock fishery during the year of capture.

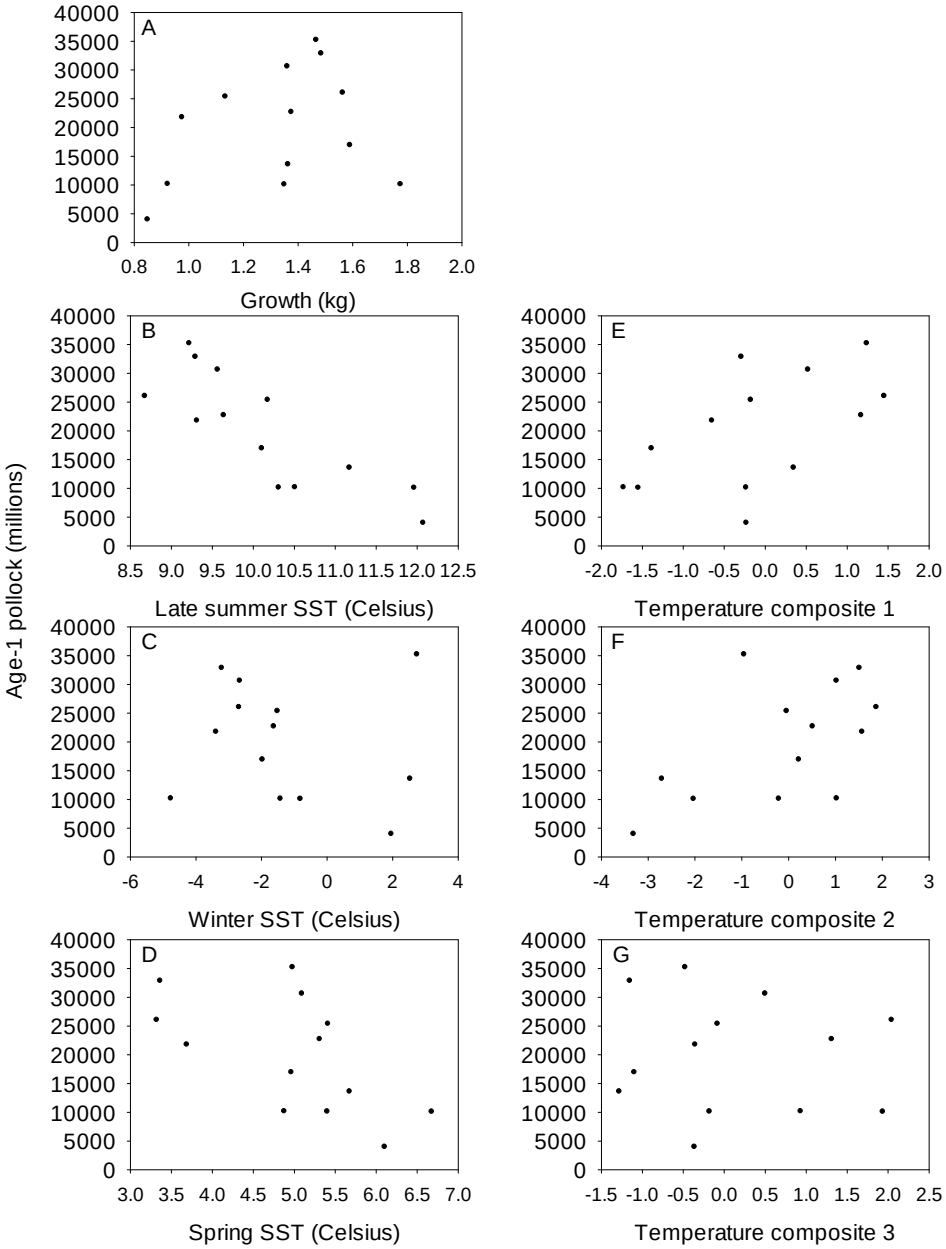

Figure 3.6. Relationship between age-1 pollock recruitment and predictor variables. Predictor variables include chum salmon growth (A), late summer sea surface temperature (SST) (B), winter sea surface temperature (C), spring sea surface temperature (D), the temperature composite 1 index (E), the temperature composite 2 index (F), and the temperature composite 3 index (G).

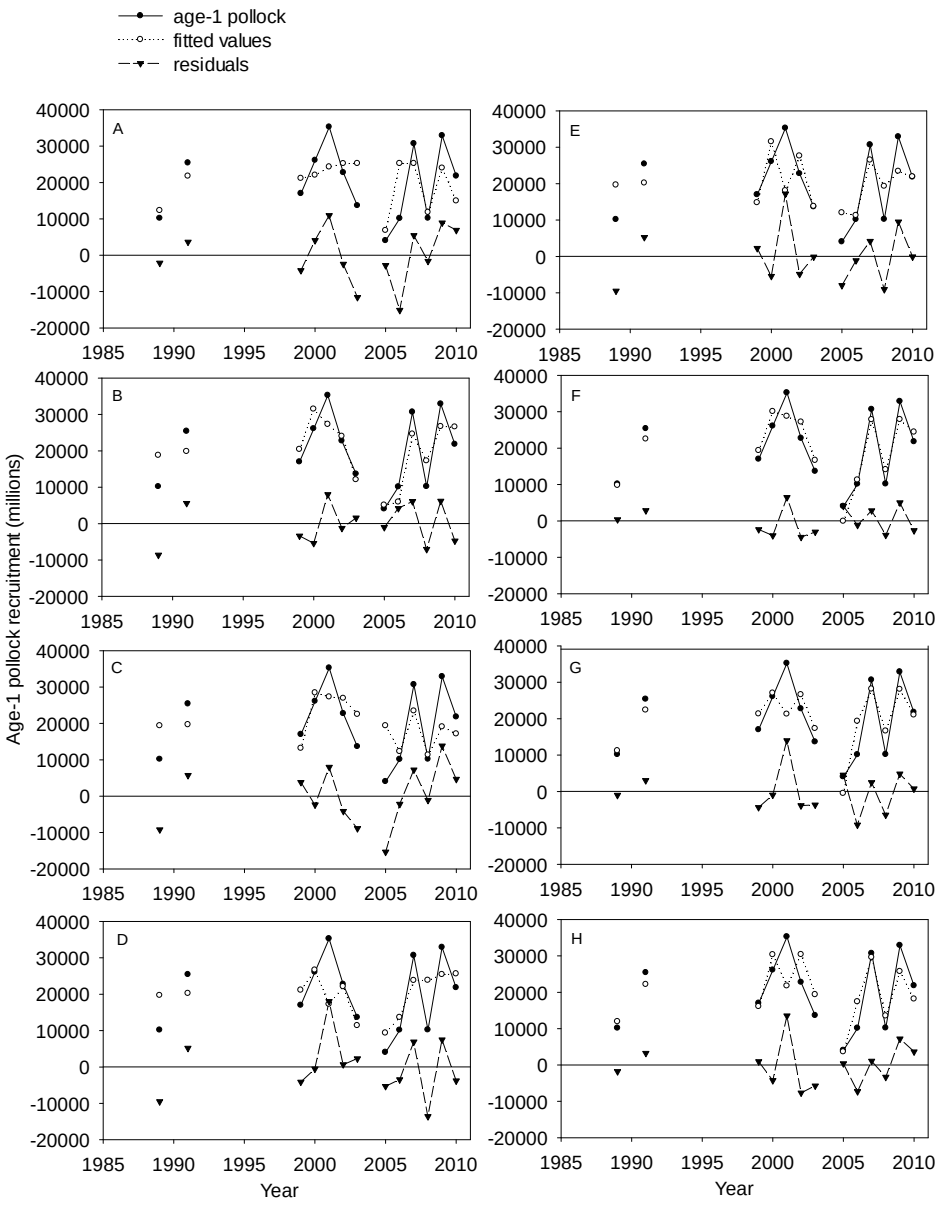

Figure 3.7. Age-1 pollock recruitment estimates, fitted values, and residuals from model A (A), model B (B), model C (C), model D (D), model E (E), model F (F), model G (G), and model H (H) in Table 3.2.

Table 3.1. Variables used to estimate the growth of age-0.3 male chum salmon bycaught in the pollock fishery in the eastern Bering Sea.

Year	$L_{age-0.3^+}$	$S_{age-0.3^+}$	$\hat{L}_{t,age-0.3^+}$	$\hat{L}_{t,age-0.3}$	$\tilde{L}_{t,age-0.3}$	$W_{t,age-0.3^+}$	$\hat{W}_{t,age-0.3^+}$	$\hat{W}_{t,age-0.3}$	$\tilde{W}_{t,age-0.3}$	$\tilde{G}_t$
1988	623	2.97	629	519	514	3.50	3.37	1.66	1.73	1.78
1990	577	2.83	602	512	492	2.53	2.55	1.41	1.40	1.13
1998	636	2.96	627	532	539	3.49	3.64	1.98	1.90	1.59
1999	636	2.91	617	530	547	3.65	3.65	2.09	2.09	1.56
2000	603	2.82	600	509	512	3.23	2.99	1.63	1.76	1.47
2001	571	2.88	610	491	460	2.49	2.45	1.10	1.11	1.38
2002	645	2.91	616	546	572	3.80	3.84	2.46	2.43	1.36
2004	586	2.74	583	520	522	2.45	2.69	1.76	1.60	0.85
2005	596	2.87	608	515	504	2.93	2.87	1.55	1.58	1.35
2006	599	2.85	604	509	505	2.91	2.92	1.55	1.55	1.36
2007	569	2.71	576	504	498	2.37	2.41	1.47	1.45	0.92
2008	616	2.77	589	499	521	3.23	3.23	1.75	1.75	1.48
2009	575	2.68	571	502	505	2.57	2.50	1.55	1.60	0.98

Note: sample sizes by year were 31 (1988), 29 (1990), 26 (1998), 17 (1999), 36 (2000), 27 (2001), 18 (2004), 42 (2005), 41 (2006), 28 (2007), 31 (2008), and 42 (2009).

Table 3.2. Pearson correlation coefficients relating age-1 pollock recruitment (*t*), growth (kg) of age-0.3 chum salmon (*t*-1), summer sea surface temperature (SST) (*t*-1), TC1: temperature composite 1 index (*t*), TC2: temperature composite 2 index (*t*), and TC3:temperature composite 3 index (*t*) for years 1989, 1991, 1999–2003, 2005–2010. Bold values indicate statistical significance at the 95% level.

	Recruitment	Growth	SST	TC1	TC2
Growth	0.31				
SST	**-0.82**	-0.37			
TC1	**0.57**	0.32	-0.52		
TC2	**0.56**	0.18	**-0.84**	0.09	
TC3	-0.08	-0.03	-0.03	0.11	0.2

Table 3.3. The regression models describing age-1 pollock recruitment (R) as a function of growth (kg) of chum salmon (G) during the last year at sea, sea surface temperature (SST), and the temperature composite indices (TC1, TC2, and TC3). Growth was estimated for a portion of the immature age-0.3 male chum salmon sampled from the bycatch of the pollock fishery in the eastern Bering Sea. *P*-values for the coefficient are given in parentheses. All coefficients are statistically significant at the 95% level. The asterisk indicates the model with the lowest *SIC*.

Model	Coefficients	R^2	*P*	*SIC*
A	$R_t = 5.489\left(\tilde{G}_{t-1}\right) - 5.207\left(\tilde{G}^2_{t-1}\right) + e_t$ (0.038) (0.040)	0.403	0.059	273
B	$R_t = -0.824\left(SST_{t-1}\right) + e_t$ (<0.001)	0.679	<0.001	262
C	$R_t = 0.567\left(TC1_t\right) + e_t$ (0.035)	0.321	0.035	272
D	$R_t = 0.563\left(TC2_t\right) + e_t$ (0.036)	0.317	0.020	272
E	$R_t = 0.623\left(TC3_t\right) + e_t$ (0.017)	0.388	0.017	270
F	$R_t = 4.017\left(\tilde{G}_{t-1}\right) - 3.999\left(\tilde{G}^2_{t-1}\right) - 0.735\left(SST_{t-1}\right) + e_t$ (0.006) (0.006) (<0.001)	0.853	<0.001	257*
G	$R_t = 5.132\left(\tilde{G}_{t-1}\right) - 4.940\left(\tilde{G}^2_{t-1}\right) + 0.492\left(TC2_t\right) + e_t$ (0.017) (0.021) (0.030)	0.583	0.010	269
H	$R_t = 4.607\left(\tilde{G}_{t-1}\right) - 4.441\left(\tilde{G}^2_{t-1}\right) + 0.499\left(TC3_t\right) + e_t$ (0.032) (0.036) (0.032)	0.631	0.015	269

Table 3.4. Summary statistics for age-1 pollock recruitment models in Table 3.3. Statistics include degrees of freedom (*df*), coefficient of variation (*CV*), coefficient of determination (R^2), *F*-statistic, *P*-value of the *F*-statistic, and Schwarz's information criterion (*SIC*).

	Model							
Statistic	A	B	C	D	E	F	G	H
df	11	12	12	12	12	10	10	10
CV	0.402	0.282	0.410	0.411	0.390	0.209	0.330	0.331
R^2	0.403	0.679	0.321	0.317	0.388	0.853	0.636	0.631
F	3.71	25.4	5.68	5.58	7.59	19.3	5.82	5.70
P-value	0.06	<0.001	0.04	0.03	0.02	<0.001	0.01	0.02
SIC	273	262	272	272	270	257	269	269

Chapter 4 General Conclusions

In this study, seasonal and annual growth time series derived from historical scale collections were used to (1) better understand the occurrence of density-dependence impacting growth in different life history stages of Chum Salmon (*Oncorhynchus keta*) from southeast Alaska (SEAK) and Washington (WA) and to (2) assess the value of stage-specific Chum Salmon growth as a proxy for ocean productivity and predictor of Walleye Pollock (*Theragra chalcogramma*) recruitment, hereafter called Pollock, and the recruitment strength to age-1. Specifically, I investigated the influence of climate and population abundance on the stage-specific length-based growth patterns of 2 Chum Salmon populations from the eastern North Pacific Ocean. Using similar techniques, I also developed an index of weight-based growth of Chum Salmon bycaught in the Pollock fishery, which was subsequently used as an indicator of ocean productivity. This index of growth, summer temperature, and 3 new temperature composite indices were evaluated as predictors of the recruitment strength of Pollock to age-1 in the eastern Bering Sea.

Evidence for density-dependent growth was observed for both stocks. Even though the performance in forecasting of all models left room for improvement, the results of this study still indicate when and where growth of Chum Salmon may be regulated by density-dependence and environmental influences. The fish from these different stocks appear to occupy slightly different habitats. For example, in contrast to the southern SEAK Chum Salmon, WA Chum Salmon may not migrate north to the Gulf

of Alaska (GOA) during the first fall and winter at sea, but instead may migrate west, thus experiencing very different rearing conditions than their Alaska conspecifics.

I tried using Asian Pink (*O. gorbuscha*) and Chum Salmon abundances as a predictor in the immature growth model since other studies have indicated that Asian Pink Salmon may impact North American salmon performance (Ruggerone and Nielsen, 2004). However, Asian Pink and Chum Salmon were only statistically significant in the 2nd-immature Fish Creek model, but not as significant as the North American abundances. There might be some interaction between these populations if the Fish Creek Chum Salmon as age-0.2 immatures migrate into the central North Pacific Ocean or the Bering Sea.

Density-dependent growth was evident during the juvenile life stage for the Fish Creek stock but not the Quilcene River stock. The mid-juvenile growth of Fish Creek Chum Salmon was negatively related to the estimated number of juvenile Pink Salmon from SEAK to the Alaska Peninsula. A 1 standard deviation change in juvenile Pink Salmon abundance resulted in a 0.521 SD or 3.5 mm reduction in growth. For fish of 228 mm length, this is only a 1.5% reduction in growth and may not influence survival. However, further investigation is needed to understand the influence of salmon abundances on the survival of juvenile Chum Salmon. For example, 1 way to assess the influence of density-dependent growth on over wintering survival is to overlay the frequency distributions of scale radii of juvenile salmon sampled at sea and the same scales radii distances of adults from the same brood. This would indicate the percent and

absolute difference in scale radii before and after winter to help determine whether a 1.5% change in length would significantly reduce survival.

Climate-driven environmental conditions during the juvenile stage are an important determinate of overwintering survival in salmon (Beamish and Mahnken, 2001; Martinson et al., 2009). Using the scale-derived growth data, I found that the late juvenile growth of Fish Creek Chum Salmon was favored by reduced winds during the fall. Wind speed during the early fall may be indicative of a fall phytoplankton bloom in the northern GOA, which in turn will have an effect on the amount of prey available for salmon prior to winter. Therefore, it might be beneficial to consider evaluating fall wind strength as a predictor for brood strength in models forecasting marine survival and returns of Pacific salmon.

One of the main concerns of the results of these multivariate time series models for Chum Salmon growth was the failure of the models to explain the increase in immature growth and adult body size during the 1990s. Climate was an important factor influencing immature growth after accounting for the influence of population abundance. The 1st- and 2nd-immature year growth increased with warmer summer SST in the eastern North Pacific Ocean and a negative Pacific Decadal Oscillation phase during winter. These results indicate that the carrying capacity for Chum Salmon in the ocean can vary with climate and has not reached a point where carrying capacity is reduced with warming. However, these models did not perform well for the reserved samples that corresponded with the year of the final adult size and immature growth increases from mid-1990s to mid-2000s. In the future, I would recommend including an index for

chlorophyll a, phytoplankton density, zooplankton density, and a prey item as predictors in the growth models. Some of the data may be acquired by updating the zooplankton time series compiled by Sugimoto and Tadokoro (1997) from various ocean surveys from the 1970s to the early 1990s. Alternatively, zooplankton, phytoplankton, and chlorophyll time series collected from the Seward Line in the GOA may be available from scientific staff maintaining the collection (http://www.sfos.uaf.edu/sewardline/index.html). An additional source for indexing primary productivity is the SeaWiF satellite images (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). The magnitude and location of phytoplankton blooms could be identified and quantified by digitizing the areas of chlorophyll indexed by the satellite images. The best possible predictors are likely a combination of physical and biological factors.

A variety of alternative models were designed/created but not presented in this dissertation. For the Chum Salmon growth models, a state space equation was used to capture variation in the residuals as integrated with the climate indices. However, the coefficients of the state space models were either unobservable or uncontrollable. The time series were likely too short and variable for this method. Also, I tried modeling the residuals of the regression models using a vector autoregression (VAR) model without the climate indices. Interestingly, only 1 model had a significant coefficient, a lag 1 for the 1st-immature growth of Chum Salmon from Fish Creek. Including climate in the VAR model resulted in a greater number of significant coefficients for the residuals and climate. Thus, additional underlying processes were unearthed when adding climate indices to the error correction model. For the Pollock model, I tried to induce linearity in

the relationship between Pollock recruitment and Chum Salmon growth by transforming both and separately the predictor and response variables using the logarithm and natural logarithm. However, the relationship remained nonlinear. Future modeling efforts on this and other salmon growth time series may benefit from using other statistical methods. Further analysis should consider running a simultaneous system of equations for Fish Creek and Quilcene River, males and females, and summer and fall runs. State space modeling may work for a different set of growth time series that are longer and less variable.

In an effort to support the Pollock stock assessment in the eastern Bering Sea, Martinson et al. (2012) developed the temperature change (TC) index that indexed thermal conditions during the late summer age-0 phase and early spring age-1 phase. The TC index was used to describe the expectation of higher or lower than average recruitment to age-1 for Pollock and Pacific Cod (*Gadus macrocephalus*) in the eastern Bering Sea (Martinson et al., 2012). In this dissertation, the TC index was expanded to include thermal conditions during the winter between the age-0 and age-1 stage and the effects of temperature during each stage was weighted equally by normalizing each temperature time series prior to the construction of the TC indices. Since the spring SST was negatively correlated with recruitment rather than positively correlated with recruitment and there was no relationship between winter SST and recruitment, the TC indices explained less of the recruitment than the summer SST. Nonetheless, the TC index should be revisited to include the mechanism for spring SST to relate negatively with age-1 recruitment and determine the relative weights of SST on recruitment at

various life stages. It is important to note that the original TC index in Martinson et al. (2012) was more strongly correlated with groundfish recruitment than late summer SST. However, in more recent years of more highly variable SSTs, the summer SST was more significant than the TC index in explaining Pollock recruitment.

Using scale-based growth data, I established Chum Salmon growth as a biological indicator of the recruitment strength of Pollock to age-1 in the eastern Bering Sea. Chum Salmon growth was a significant nonlinear predictor of Pollock recruitment to age-1. My results indicate that Pollock experience optimum environmental conditions when co-occurring age-0.3 Chum Salmon incur intermediate amounts of growth. The exact mechanism for this nonlinear relationship is still not understood. To further investigate the value of Chum Salmon growth as a biological proxy for ocean rearing conditions favorable for Pollock, I suggest developing an index of growth in body weight using scales and biological information from adult Chum Salmon originating from a single river (i.e., Yukon River) to reduce variations in growth that may impact the value of this biological index for Pollock recruitment success.

Conclusions

Salmon are sensitive to environmental change and these changes are recorded in the growth patterns on their scales. In this dissertation, I disentangled some of the simultaneous influences of climate and population abundance patterns on the growth of Chum Salmon for 2 geographically separated populations from the eastern North Pacific Ocean. The entanglement of multiple factors contributing to growth supports the use of

salmon growth as a biological indicator for ocean productivity and the recruitment of Pollock. Salmon growth may also index habitat quality used by other species. These results support the use of salmon and their scales as data recorders of the productivity and quality of marine ecosystems as rearing environments for fish.

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